THE
CHANGING FLORA
OF
BRITAIN

THE CHANGING FLORA OF BRITAIN

BEING THE REPORT OF THE

CONFERENCE

HELD IN 1952 BY

THE BOTANICAL SOCIETY OF THE BRITISH ISLES

EDITED BY

J. E. LOUSLEY

1953

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CONTENTS

EDITORIAL NOTE

The papers read at the third Conference arranged by the Botanical Society of the British Isles proved of such outstanding interest and importance that the Council of the Society decided to make them available to a wider public. The pages of this volume include a very high proportion of information and original thought not available elsewhere.

" The Changing Flora of Britain " was selected for the title of the Conference as a theme likely to bring together studies of very diverse aspects of the study of British botany. The record in this book will show how successfully this was achieved and how each paper contributed to the general theme. Approaches to the subject include the evidence derived from ecology, palaeobotany, phytogeography, the recent introduction and spread of aliens, and the special study of trees and shrubs. The papers have been arranged for publication in the sequence stated—the order in which they were delivered at the Conference is set out in the Programme printed on the next two pages. The valuable contributions of botanists from abroad and of a zoologist have been included in appropriate positions in the book.

Scientific names used in the papers are those selected by the speakers and it has not been thought advisable to attempt to standardise them. Where authors' names are omitted the nomenclature is generally that adopted in current British ecological work as given in the *Check List of British Vascular Plants* (1946: *J. Ecol.,* **33**, 308-347) and Clapham, Tutin and Warburg's *Flora of the British Isles,* 1952. Distribution maps are printed as submitted by the contributors.

The arrangements for the Conference were in the hands of the Meetings Committee of the Society and most of the work fell on Dr. J. G. Dony, Honorary Field Secretary, and Mr. W. R. Price, Honorary Assistant Secretary. The success of the Conference was due to their energy and enthusiasm, together with that of the other officers and members who assisted in the organisation. We are indebted to the British Council for grants which made it possible to invite Dr. P. Jovet and Dr. Ch. H. Andreas to come to the Conference to read their papers. We are also grateful to all the other people and bodies who assisted.

I should like to take this opportunity of acknowledging the assistance of all those who kindly gave permission for reproduction of maps or base maps used in connection with the illustrations. Thanks are also due to the members of the Publications Committee who read the proofs of this book and to Mr W. R. Price who prepared the index.

J. E. Lousley.

CONFERENCE PROGRAMME 1952

THE CHANGING FLORA OF BRITAIN

FRIDAY, April 4th

First Session

10.30 a.m. The Significance of a Changing Flora
The President: The Rev. Canon C. E. RAVEN

11.00 The Historic Element in our British Flora: Full-Glacial and Late-Glacial Floras
Dr. H. GODWIN

11.50 A Changing Flora as shown in the Study of Weeds of Arable Land and Waste Places
Sir EDWARD SALISBURY

12.45 p.m. Interval for Luncheon

Second Session

2.15 Exhibit: British Late-Glacial Plants
Mr. D. WALKER and Mr. R. WEST

2.30 Natural Factors contributing to a Change in our Flora
Prof. T. G. TUTIN

3.10 Glacial Relics in the Netherlands
Dr. CH. H. ANDREAS (Groningen).

3.25 The Continental Element in our Flora
Dr. S. M. WALTERS

4.15 Interval for Tea

Third Session

5.00 Exhibit: Some Post-war Additions to the British Flora
Mr. R. D. MEIKLE

5.15 The North American and Lusitanian Elements in our Flora
Dr. J. HESLOP-HARRISON

6.00 Exhibit: Some Parallels between British and Scandinavian Plants
Dr. A. MELDERIS

6.15 Exhibit: Subfossil and Present-day Distributions of some Scandinavian Alpine Plants and their Interpretation
Dr. E. DAHL (Oslo).

SATURDAY April 5th

First Session

10.30 a.m. Human Factors contributing to a Change in our Flora
Prof. A. R. CLAPHAM

11.15 Exhibit: *Epilobium adenocaulon* in Britain
Mr. G. M. ASH

11.30 The Zoologist's Apprcach to a Changing Flora
Dr. MAURICE BURTON

12.15 p.m. Exhibit: Possible Human Historical Factors in the Distribution of *Eriophorum latifolium* and other Species in the Conway Valley
Dr. E. HUGHES

12.30 Interval for Luncheon

Second Session

2.00 A Changing Flora as shown in the Status of our Trees and Shrubs
Dr. E. F. WARBURG

2.55 The Recent Influx of Aliens into the British Flora
Mr. J. E. LOUSLEY

3.45 Exhibit: Wool Aliens
Dr. J. G. DONY and Mr. J. E. LOUSLEY

4.00 Interval for Tea

Third Session

4.45 Exhibit: Is the Box Tree a Native of England?
Mr C. D. PIGOTT and Dr. S. M. WALTERS

5.00 Exhibit: The Changing Botanists of Britain
Mr. D. E. ALLEN

5.15 The Conservation of British Vegetation and Species
Sir ARTHUR TANSLEY

6.00 Closing Remarks by the President

SUNDAY, April 6th

FIELD MEETING TO THE NEIGHBOURHOOD OF ASHFORD (KENT) TO STUDY THE STATUS OF *THLASPI ALLIACEUM*

(The programme printed above is as circulated before the Conference. It was carried out as stated. One additional paper was read during the Third Session of Friday, April 4th:—

Some Recent Modifications in the Flora and the Vegetation of the Valois.

Dr. P. JOVET

Two additional exhibits were included in the Second Session of Saturday, April 5th:—

Exhibit: Man's Influence on Hybridisation in *Crataegus*
A. D. BRADSHAW

Exhibit: *Epilobium pedunculare* A. Cunn. in Britain
Miss A. J. DAVEY)

LIST OF MEMBERS AND GUESTS WHO ATTENDED THE CONFERENCE, April 4 and 5, 1952

(The following list includes only those who attended the meetings held at the Royal Horticultural Society's New Hall, Greycoat Street, Westminster, London, S.W.1. It is known to be incomplete and we have been unable to give the names of some of the guests in full).

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G Mrs Heslop-Harrison
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THE SIGNIFICANCE OF A CHANGING FLORA

The Rev. Canon C. E. Raven.

The President of the Society in opening the proceedings of the Conference read the following paper:—

It is a terrifying honour, for one whose claims to the title of botanist are of the slenderest, to be asked to introduce a Conference on so large and fascinating a theme and of so distinguished and expert a personnel. Nor does the work that I have been able to do on the early students of the British flora give me as much material as might be expected. For, as you all know, the Catalogues compiled by the greatest of them, John Ray, and even the less reliable lists by Thomas Johnson or the Herbals of William Turner, John Gerard and John Parkinson, testify rather to persistence than to changes. Apart from the loss of the two fen Senecios and one or two other residents, the plants which Ray recorded so meticulously can still be found, like *Eryngium campestre* or *Veronica spicata,* in the same precise localities as in his day. Some of his aliens have been lost and of the very many more that have since been added it is by no means usual for them to establish themselves permanently; species like *Epilobium angustifolium,* or *Senecio squalidus* or *Juncus tenuis* are a relatively small number. Some years ago I sent to Mr. A. J. Wilmott a list of additions and corrections to Clarke's First Records, and am probably not alone in hoping that a fully revised edition of that valuable work will soon be undertaken. But, all things considered, the number of emendations is not large.

Before leaving early records I may perhaps report one that surprised me.

Bound up with the original manuscript of Mouffet's *Theatrum Insectorum,* now in the British Museum, is a holograph letter to Thomas Penny, Mouffet's friend and the principal author of the volume, from his friend, the Somersetshire doctor William Brewer, In this, along with information about insects, is a detailed and exact account of a weed, which had appeared in his garden and which from the description of its seed-vessel and seed-dispersion and from its name, is beyond any doubt *Oxalis corniculata.* It was interesting to discover that this denizen, which is commonly regarded as a recent arrival, was a garden weed in the west country nearly four centuries ago—in or about 1585.

Obviously, with the colossal changes that have taken place in speed and range of transport, the invasion of Britain by aliens of every kind has been enormously increased. Problems like the assortment of mid-European species in the bomb-crater at Box Hill, or the arrival and hybridising of Australian *Junci* in the

gravel-pits at Eaton Socon, or the strange appearances of the New Zealand *Epilobium pedunculare* in Northern Ireland, on Plynlimmon and in Ross-shire almost simultaneously, seem to defy explanation. Those like the American denizens of lease-lend carrot fields at the close of the war, or the Australasian concomitants of shoddy, or the mixed intruders which make the sidings at Burton such a happy hunting-ground, are more likely to yield permanent additions. But I confess that such obviously human-borne seedlings do not seem to me to deserve much consideration. I am not convinced that we ought not to advocate definite action to prevent their settlement—instead of which, alas, I waste my time in painting their pictures. There ought at least to be a clearer policy in determining their claim to inclusion in our flora.

Among these casual introductions is one—*Spartina alterniflora*—which though of little scientific importance in itself seems very significant in its offspring. The original species has apparently almost died out—why, in view of its vitality on the mud-flats in Massachusetts Bay, is difficult to explain. But in producing *Spartina Townsendii* it has raised an issue not only for the geographer but for the theoretical biologist. Of its immense vigour those of you who know how seriously its appearance off the mouth of the Manchester ship-canal endangered our national safety in the war will be fully aware. It is obvious that like other famous hybrids, *Poa annua* and *Galeopsis Tetrahit* for example, it has a vitality and invasiveness out of all proportion greater than its parents. One is obliged to ask what part such hybrids have taken in the whole course of evolution? What is the cause of their amazing efficiency? and how far do they supply an analogy for similar developments in zoology? I have long suspected that fertile hybrids between distinct species might be a not unimportant factor in the process of creation, but the only zoological example that I have investigated—the moth now called *Arenostola brevilinea*—if a hybrid is one whose metamorphosis makes it very ill-suited for laboratory study. Botanical geneticists should have a better chance of investigating such problems.

At risk of seeming to go beyond the scope of our programme—I must add that, while the changes in our flora by invasion give rise to a number of fascinating ecological, physiological and chemical problems which deserve full investigation, for my own part I must draw attention to changes which raise rather different issues.

Here is the point to which I specially desire to draw attention—the changes taking place in our flora not by introduction from outside, nor by changes in the status and distribution of native species, but by the extreme variability of many of our most familiar groups. In Britain we have a relatively small area, widely varied in soil, altitude, character and climate, closely

studied over a long period, and the home of a remarkable number of still varying aggregates. I need hardly remind you of the great apomictic groups—*Hieracium, Taraxacum, Rubus, Rosa, Alchemilla,* and of the (usually) normally sexed groups *Ranunculus aquatilis* agg., *Viola, Euphrasia, Polygonum, Salix, Orchis, Carex flava* agg., *Bromus secalinus* agg., *Festuca* and *Poa.* But it is worth drawing attention to the fascinating problems which these present not only to the systematist but to the biologist, and to the need for far wider and deeper study of them than has yet been made.

We all know how elaborate has been the work of students like Ley and Marshall and Pugsley on the *Hieracia,* or of Riddelsdell, Watson and a host of others on the *Rubi;* we know, too, of the hundreds of named forms in both genera and of the enormous difficulties of identification and nomenclature that have resulted. For "our changing flora" it is pretty evident that new varieties are still being discovered and indeed are almost certainly coming into existence. (I cannot speak with knowledge of *Rubus*: but my son's work clearly indicates this in *Hieracium*). I should be the last to decry the value of this intensive study or of the interest of the questions that arise from it: those who dismiss apomictic variants as infinite and meaningless can hardly have given the subject much attention. But nevertheless it remains true that quite insufficient work has been done in demonstrating what are the characteristics that are genetically significant, and it is not easy to show which of the differentia employed (for example in Pugsley's great monograph) represent a real variation and which are merely due to local and environmental influences. The fact is that almost no cytological and physiological study of the genus has been carried out in this country, and that even the cultivation of the varieties has been casual and directed chiefly towards the noting of its superficial effects.

Nor does the treatment of the genus by biologists reveal much except guess-work and speculation. When for example Professor Stebbins in his joint monograph on the American members of the genus *Crepis* deals with its apomictic species he is content to describe the general problem of apomixis, to dismiss the details of the variation as unimportant and to claim that the loss of sexual propagation and the consequent greatly increased variability indicates the last struggle of a type which like his one example, *Houttuynia cordata,* is on its way to extinction. When in his large and more recent volume, *Variation and Evolution in Plants,* pp. 396-419, he sums up the subject, he supports this verdict by a piece of remarkable special-pleading. For he claims that whereas sexually reproduced forms have both a wider range of gene-combination and the possibility of mutations, apomicts are dependent only upon the combinations in the original parents from which they as hybrids are derived. He omits altogether the two facts (1) that even if apomicts have theoretically a smaller

range of combination yet in fact they do display a much larger incidence of variation and in consequence a much greater power of adaptability, and (2) that apomicts, as C. H. Ostenfeld has demonstrated, are as liable to mutation as any other plants. Moreover, though there may be in *Houttuynia* an example of a dying type, it is ridiculous to speak of *Hieracium* or *Rubus* in such a category. It would, in fact, be much easier to argue that, although no doubt the stabilising influence of sex-reproduction may generally be of value to a species, there is plain evidence that, in an environment like Britain where soil, climate, altitude and other conditions vary so widely, a plant that has developed apomictic reproduction and the consequent increased power to perpetuate variations has gained more than it has lost.

Obviously the question whether biologically apomixis is to the advantage or disadvantage of the species is one on which presuppositions about the worth of sexual reproduction are wholly insufficient. Professor Stebbins' guess is as good as any other, but not any better. And the analogies from *Drosophila* which have overshadowed and dominated Genetics too long are in this case at least meaningless.

Obviously, too, we who have so large a number of highly variable species are in a strong position. Instead of following contentedly the conclusions of Scandinavian, Danish and German research we should ourselves mobilise a team which could tackle the problems, genetical, cytological, physiological, ecological and chemical, and see whether out of the available mass of material we can not only reach a settled nomenclature and taxonomy (this is relatively unimportant—little more indeed than bare collecting) but make a serious contribution to the general problems of evolution. It is, to any botanist who comes over to botany from zoology, a sad thing to see how relatively poor has been the contribution of botanists to the more general study of science and to the answering of the questions on which they ought to have something important to say.

May I close these precarious and perhaps impertinent remarks by a personal confession? As primarily an ornithologist I have spent many years pleading that the business of adding new and casual visitors to the Fair Island list or of splitting the Tits into insignificant subspecies was a relatively childish and scientifically valueless pursuit—as compared at least with the study of behaviour. I cannot but make a similar plea to a Conference like this. By all means let us collect and identify and classify our flora, and note additions to it, and calculate their chances of survival. But let us remember that this is only preliminary investigation: we do not learn from it anything of scientific value, unless we use our experience to throw light upon the problems of the relationship of the plant to its environment, of its adaptation and survival, and of the parts played by nature and nurture in its constitution.

And here for us in this Society there is a special point to hold in mind. Botany, as I was told recently by a professional botanist who is a colleague and friend to many of us, has always been an amateur's field of study. "This," he said, "has its drawbacks if it means that the professional is left to do the strictly scientific work in isolation." We do not, I fear, make full or wise use of the help that only the man whose whole life is spent on plant-problems can give us. I hope that this Conference, bringing together so large and varied a group of botanists, may do something to bridge the gap that is always liable to open between the field-worker and the expert, the amateur and the professional.

NATURAL FACTORS CONTRIBUTING TO A CHANGE IN OUR FLORA

T. G. Tutin.

I find this a difficult subject to discuss because of the impossibility of drawing a reasonable distinction between 'natural' and 'artificial' factors. It is rather like asking "When is an introduced plant not an introduced plant?" There are various unsatisfactory answers to that question such as "When it was not introduced by man", or "When it has been here as long as anyone knows". Now that it is realised that our records go back for less than a tenth of post-glacial time and that man and other animals have been carrying plants backwards and forwards at least since the end of the Ice Age, it is obvious that these distinctions are neither real nor natural. One may perhaps attempt to distinguish between deliberate introductions by man and unintentional introductions. On this basis one may say that natural factors contributing to a change in our flora are all those other than the deliberate actions of man.

Whatever one's views about 'natural' and 'artificial' or 'native' and 'introduced', it is clear that two kinds of change can be distinguished: qualitative change and quantitative change. Since the factors involved are largely different these must be considered separately.

The three main causes of qualitative change in any flora are evolution, climatic changes and the introduction or extinction of species. The processes of evolution produce the most fundamental, though probably the slowest, changes and since a good deal is now known about them I will spend a short time giving you a few examples of what is going on in our flora at present. There seem to be three main processes at work. The first of these is the gradual differentiation of species through mutation and selection without change of chromosome number, producing in time what Valentine has called g-ecospecies. Then there is the well-known process of doubling, quadrupling and so on, of chromosomes, which appears often to occur in hybrids between species and probably sometimes within species. This produces polyploid series and gives rise to a-ecospecies in Valentine's convenient terminology. Finally, there is the less well-known and apparently rarer process of aneuploidy which entails the gain or loss of one or a few pairs of chromosomes and also gives rise to a-ecospecies.

A comparatively late stage in the first process is to be seen in the primrose (*Primula vulgaris* Huds.), oxlip (*P. elatior* (L.) Hill) and cowslip (*P. veris* L.), and a somewhat earlier stage in

the red and white campions (*Melandrium rubrum* (Weig.) Garcke and *M. album* (Mill.) Garcke). What appear to be still earlier stages in differentiation which, if my guess is right, is taking place before our eyes in this country, are shown by *Veronica spicata* L. and *Helianthemum canum* (L.) Baumg. The former is on the Continent a variable species showing a distinct preference for a continental climate. In this country, on the other hand, there are two distinct populations differing somewhat morphologically and occupying quite separate areas. Subspecies *spicata* is a small plant of dry chalky heaths in East Anglia where rainfall is low and the annual range of temperature great: subspecies *hybrida* (L.) E. F. Warb. is a larger plant with a strongly oceanic distribution in W. England and Wales where the rainfall is high and the annual range of temperature small.

There seems no reason why the isolation of these two should break down and every reason to suppose that as long as it does not, differentiation will continue. There does not appear to be any published information about whether these subspecies are completely interfertile, though recent experiments by Dr. Walters indicate that this is so.

Helianthemum canum is another somewhat similar case, though here the Continental as well as the British distribution is markedly discontinuous and, as far as my observations go, each population differs somewhat from the others. Plants from Teesdale, and Scout Scar near Kendal, may be taken as typical of the kinds of differences which occur and are maintained in cultivation.

In the former, the oblong leaves are nearly glabrous on top and reach a length of 10 mm. The stems and sepals have little anthocyanin and the petals are pale yellow, about 5 mm. long and strongly reflexed. The longest branches under garden conditions grow about 23 cm. a year and the flowers regularly open 7-10 days before those of the Kendal plant when the two are grown side by side.

The Kendal plant is densely grey-tomentose and the ovate leaves reach a length of 7 mm. The stems and sepals have abundant anthocyanin and the petals are deep yellow, about 7 mm. long, and spread horizontally. The longest branches grow about 8 cm. a year, but the majority of them die back in autumn.

Both populations have the same chromosome number ($n=11$) and appear normally to be selfed and to breed true for the characters mentioned.

Populations of this kind are presumably derived from a formerly widespread and variable species; they seem to me to indicate clearly one method of the production of very local endemics, such as are commonly found in unglaciated regions where there has been far more time for speciation to occur than in N. Europe.

Evolution through polyploidy, when it occurs, is a more striking process because of its abruptness. One of the best known recent examples in this country is, of course, *Spartina Townsendii* H. & J. Groves, which arose in Southampton Water in the latter half of last century. *S. alterniflora* Lois., an American species, became established there, hybridised with our native *S. maritima* (Curt.) Fernald, and the hybrid, through chromosome doubling, gave rise to *S. Townsendii,* a vigorous plant which is far more successful than either of its parents. This example illustrates the great importance for this method of evolution of any factor (e.g. climatic change or human interference) which brings together allied but geographically isolated species. This has undoubtedly been one of the major factors involved, and it is probably true to say that a-ecospecies are produced most commonly in periods of drastic change while g-ecospecies develop in ages of comparative stability.

Apomixis, and particularly the type known as agamospermy or the production of seeds without fertilisation, is a common, though rather minor, factor involved in the development of new species in some genera in our flora. This process enables hybrids, notably triploids and pentaploids, which would otherwise be sterile, to reproduce successfully, and also produces populations which differ constantly but only to a small extent from others. It largely accounts for the great number of "small" species in genera such as *Hieracium* and *Rubus*. It also occurs, though to a lesser extent, in a great number of other genera, for example *Ranunculus, Potentilla, Sorbus,* and *Poa.*

In certain genera, particularly *Carex,* aneuploidy is far commoner than polyploidy. Miss E. W. Davies has shown, for instance, that it has probably played a large part in the isolation of *Carex flava* L., *C. lepidocarpa* Tausch and *C. demissa* Hornem. from one another. The same process appears to be going on in *C. caryophyllea* Latour. where Miss Davies has found $n=33$ and 34, while Tischler records $n=31$ from continental plants. These numbers are associated with considerable size differences and other smaller morphological differences.

Turning now to the question of climatic changes, it is important to bear in mind how profound these have been even during the last 12,000 years and what a great effect they have had on the composition of our flora. Dr. Godwin has made this point clear (see pp. 59-74). There is no reason to suppose these changes have ceased, and we would expect some of their effects to be visible. Seven species are stated to have become extinct in this country in recent times and I propose to examine for a moment the case of two representatives from this list, *Senecio paludosus* L. and *Trichophorum alpinum* (L.) Pers. These show some similarities in that they are both commonly stated to have been lost through drainage and they both grow in damp base-rich habitats.

Senecio paludosus formerly occurred in fen ditches in four eastern counties. Its distribution on the Continent is fairly wide, extending north to S.E. Sweden, the Baltic States and N. Russia. It is extinct in Denmark and is quite absent from Norway, the west of France and the whole of Portugal; it clearly has a somewhat 'Continental' type of distribution. Fen ditches still exist in abundance, and in S. Sweden the plant can be seen growing in ditches at the margins of fen woods, a type of habitat which is not uncommon in this country. It seems clear to me that it occurred in East Anglia as a relic of a period when our climate was more continental, and that its diminution and ultimate extinction was due primarily to climatic change, though the final blow may have been the destruction of one particular habitat or even the excessive attention of some 19th Century botanists.

Trichophorum alpinum is predominantly a northern species of lowland habitats which thins out in the south of its range (France, Switzerland, etc.) where it seeks refuge in the mountains and, according to Hegi, reaches altitudes of 2,000 m. It is not so continental in its distribution as *Senecio paludosus,* but in Scandinavia increases in abundance towards the east, and is entirely absent from Iceland. This continental tendency is more marked in the southern part of its range. It formerly occurred in Angus, which has a less oceanic climate than most of Scotland. Its extinction and its absence from other apparently suitable areas such as the damp, peaty, base-rich habitats which are not infrequent in the neighbourhood of Ben Lawers all suggest that it is another victim of a changing climate.

It seems impossible to get any satisfactory evidence about new arrivals, partly because chance plays so large a part and partly because it is never possible to say that a certain species has often before arrived in the country but has been unable to establish itself until the present.

Sir Edward Salisbury and Mr. Lousley are dealing with the influx of alien species into this country in detail, but a word or two must be said about it here as at least some plants arrive by what are known as natural means. It seems likely that *Alisma gramineum* C. C. Gmel. found its way to its one known station near Droitwich on the feet of migrating water-fowl. The fact that it grows in an artificial pond may well be due to the probably less intense competition in such a pond, which would make the initial establishment of the seedlings easier. It has survived in this place for more than thirty years and it is probably only a matter of time before it spreads to other suitable habitats.

Scutellaria hastifolia L. is another example of recent introduction by unknown but probably 'natural' agency. This also has every appearance of being a successful species in this country, as it is known to have spread considerably since its original discovery. In a garden it is all too successful and not only spreads vegetatively with great rapidity but produces an abundance of seed.

There are, of course, many examples of unsuccessful introductions, among which *Inula Britannica* L. may be mentioned. This is believed to have arrived in the same way as *Alisma gramineum* and, like the latter, became established in a man-made habitat, the margin of Cropston Reservoir near Leicester, where competition is not severe. It survived for about forty years but has now disappeared completely. It seems undoubtedly to have been some climatic factor which finally killed it, as the habitat has suffered no obvious change and there is no evidence of over-collecting. It may well have been that the summer temperatures were too low to allow adequate seed production and that the original plants reached the end of their normal life. On this point, as on so many other similar ones, there appears to be a complete lack of evidence.

It is perhaps worth pointing out that the extinction or increase in abundance of rare plants may be determined by some exceptional fluctuation in climate, while the effective establishment of a new migrant probably requires a more lasting though less striking change. It is well known to gardeners, especially after the winter of 1947, that a plant may thrive for a hundred years and then be completely destroyed by exceptionally low temperatures. It would appear to be largely the extremes and not the means of the climatic factors which are of significance in this respect.

Quantitative changes in our flora are always going on, though, of course, at varying rates; in trees they are slowest and in annuals most rapid. They are seldom noticed except among rare plants, or plants that were formerly rare.

Such changes are due to two main causes: changing climate or, in annuals, fluctuations in weather from year to year; and drastic changes in habitats, due directly or indirectly to man. The latter, though really outside the scope of this contribution, cannot altogether be separated from the former.

One of the most accurately recorded changes of this kind is the spread of *Himantoglossum hircinum* (L.) Sprengel, which has been described by Good. It confirms the statement made by meteorologists that there has been a slight but definite improvement in climate since about 1900. The decrease of *Scheuchzeria palustris* L. is probably primarily due to the same shift in climate, though it is complicated by the drainage of some of the bogs in which the plant formerly occurred. It is, all the same, clear that *Scheuchzeria* was, and still is, at its extreme south-western limit in this country. To take one former locality as an example, there are still, in spite of drainage, apparently suitable habitats for it in Shropshire. It may also be worth pointing out that some of the New Forest bogs with their abundant *Carex limosa* L. seem to meet its edaphic requirements, while it is known from Somerset as abundant remains in the peat of the Levels. Man has blamed himself too much and climatic changes not enough for the decrease or extinction of rare species.

Cyperus fuscus L. is a good example of an annual which fluctuates greatly in abundance with variations in weather from

year to year. In cultivation it is found to need a relatively high temperature for germination and sets little or no seed at Leicester in a cool summer. Man has undoubtedly caused its extinction in Middlesex, but there is otherwise no evidence for any permanent change in abundance.

Ranunculus ophioglossifolius Vill. shows similar fluctuations both in Gloucestershire and in its northernmost station on the island of Gotland in the Baltic. In both places, however, the amount of bare mud provided by the trampling of cattle seems to be an even more important factor than the weather. In cultivation at Leicester, seed was produced abundantly even in the cool summer of 1951.

Finally the dramatic spread of certain species in the last hundred years must be mentioned. Two good examples of this are *Chamaenerion angustifolium* (L.) Scop. and *Crepis taraxacifolia* Thuill. The first of these occurs as two so-called varieties, var. *macrocarpum* Syme and var. *brachycarpum* Syme. Sowerby's *English Botany* says of the former: "in borders of woods, damp places and on rocks. Sparingly, but generally distributed from Somerset and Hants. to Orkney." Of the latter it says "in damp woods and by river-sides. Much rarer than var. α, and probably either planted or escaped from cultivation. It occurs in several places in Shropshire; in N. Wales; Hampshire; by the banks of the Swale, Richmond, Yorkshire; Colinton Woods, near Edinburgh . . . . it is very commonly cultivated under the name of French-Willow or Rose-Bay."

In Lapland, var. *macrocarpum* is a common plant while var. *brachycarpum* is found only beside the railway and in similar disturbed places. It seems clear that the present great abundance of the plant in this country is due to two factors: first, the introduction of a new ecotype or subspecies and, secondly, the great increase in suitable habitats due to felling, bombing and other similar factors. It is interesting to note that var. *macrocarpum* does not appear to have spread from its original habitats and that var. *brachycarpum* is no longer cultivated in the south, but is sternly discouraged by gardeners, though it may be seen in gardens and on sale in markets in the Highlands.

Crepis taraxacifolia shows a somewhat similar state of affairs though, since it was first recorded as late as 1713, some doubt has been expressed about its status as a native plant. However, as it occurs throughout west Europe, from Spain and Portugal to N.W. Germany, it is possibly indigenous. Turning once more to *English Botany* we find its habitat and distribution given as "In chalky places and by roadsides, and in waste places in limestone districts. Local. Plentiful in Kent. It occurs also at Bookham in Surrey; in Suffolk; in the south of Essex; at Scarborough; and in Caernarvonshire". This distribution may indicate that it had recently crossed the Channel or that it was successful only in the area of high summer temperatures. Scarborough and Caernarvonshire may have been adventive localities. In any case its

distribution seems to have been much the same in 1884 (J. D. Hooker. *Student's Flora of the British Islands*). Since then it has increased in abundance greatly, either owing to climatic change, or the introduction of new ecotypes, though there is no evidence for the latter. It is now one of the two most abundant species of *Crepis* in England and Wales northwards to Yorkshire and Lancashire.

In conclusion, I would suggest that the two most important natural factors producing changes in our flora are evolution and altering climate, both very powerful and far-reaching, but both slow-acting. There is a great need for more observations about the effects of these factors, and many of these observations can be made by amateurs. The kind of thing that is needed is information about flowering, seed production, germination and survival, if possible correlated with real meteorological information, not temperatures in a Stevenson Screen, which has never been a plant habitat. This can provide the essential basis for experiments, which are perhaps best left to the professional who has usually more means, and sometimes more time, at his disposal.

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HUMAN FACTORS CONTRIBUTING TO A CHANGE IN OUR FLORA: THE FORMER ECOLOGICAL STATUS OF CERTAIN HEDGEROW SPECIES

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Some years ago Mr. Charles Elton asked me where, in this country or elsewhere, *Lamium album* was a constituent of undoubtedly natural vegetation, and I found that I could not answer his question. Similar problems about other hedgerow and wayside species had already occurred to me and I began to consider the matter more seriously. This paper embodies reflections on five such species. Since hedges are man-made habitats, and since there is a threat that they may soon become much changed floristically, I claim that my topic lies well within the subject of this conference.

Druce, in his *Comital Flora* (1932), gives the following notes on the species considered in this paper:

1. *Aegopodium Podagraria* L.
   Viatical. British. Alien. Europe. Waysides, hedges, waste ground. P. A persistent garden pest; chiefly near habitations. Lowland, up to 1300 ft. in Yorks.
   Throughout the British Isles.
2. *Chaerophyllum temulentum* L.*
   Septal. British. Hedgebanks, fields, waste places. P. Lowland, ascending to 1200 ft. in Yorks.
   All save 96, 97, 102-104, 107, 108, 110-112.
3. *Anthriscus sylvestris* (L.) Bernh.
   Septal. British. Roadsides, hedge-borders, fields under shade of trees. P. Lowland, up to 1200 ft. in Derby; 1750 ft. in Atholl; 2500 ft. on Brandon cliffs.
   Throughout Britain save Jersey and Guernsey.
4. *Tanacetum vulgare* L.
   Viatical. British. Banks, hedges, waste places. Common. P. Lowland, to 1200 ft. in Scotland.
   Throughout Britain save 51?, 69.
5. *Tussilago Farfara* L.
   Agrestal, etc. British. Clayey soils. P. Lowland, ascends from near sea-level to 1950 ft. on Highfield; 2550 ft. on Snowdon; 3500 ft. on Ben Lawers; 1900 ft. in Co. Down.
   Abundant throughout the British Isles.

All, it will be seen, are species widely distributed in the British Isles but more or less confined to secondary, man-made habitats, so that it is not clear what was their ecological status before

*This is as given in *Comital Flora*. (See also Sprague, *Proc. Cotteswold Nat. Fld. Club* for 1948, **30**, 28 (1950)). The spelling used in this paper is *C. temulum* L.—ED.

these habitats came into existence. Of *Aegopodium,* indeed, it is stated that it is not a native species. This, however, is a view which must be reconsidered in the light of recent work on the history of the British flora (e.g. Godwin, 1950). Thus Druce, again in the *Comital Flora,* writes of *Centaurea Cyanus* L.: "Agrestal. British. Native or colonist. . . . Probably of oriental origin and perhaps native in Sicily, Greece and Cyprus". Yet pollen of this species has recently been found in peat of Late Glacial age, both in Denmark (Iversen, 1947) and in this country (Godwin, 1949).

During a visit to Sweden in the summer of 1950, all the five species listed above were seen growing as constituents of little-disturbed natural vegetation, and this prompted an enquiry into their history as members of the British flora.

1. *Aegopodium podagraria* L.

During the excursion in Scania (S.E. Sweden), which preceded the 7th International Botanical Congress, *Aegopodium Podagraria* was seen on two occasions as an important constituent of the woodland ground flora. It was locally dominant in a *Carpinus-Corylus* wood near Stenshuvud close to the coast just north of Simrishamn, its associates being *Galeobdolon luteum* (f), *Anemone nemorosa* (f). *Stellaria Holostea, Oxalis Acetosella, Allium ursinum, Vicia sepium* and *Poa nemoralis.* The site was damp and the soil a heavy calcareous loam.

On the second occasion, it was seen in a mixed wood of *Fraxinus excelsior, Ulmus glabra* and *Fagus sylvatica* near Andrarum. Here, again on a damp calcareous soil, it was locally abundant with *Polygonatum verticillatum, Geum urbanum, Filipendula Ulmaria, Carex sylvatica, Geranium sylvaticum, Rubus saxatilis, Thalictrum aquilegiifolium* and *Equisetum sylvaticum,* with *Petasites albus* in great quantity nearby and a few plants of *Lysimachia nemorum* and *Carex remota.* There was no reason to doubt that *Aegopodium* was a natural constituent of these two woods. Lindquist (in Rübel, 1934), indeed, recognizes an *Aegopodium Podagraria* synusia of Swedish beech-forests, and gives its pH range as 5.6-7.2 (–7.6). *Aegopodium* also occurs as an occasional ground-flora species in Allindelille Fredeskov, a mixed deciduous wood in N. Sjaelland, Denmark, chiefly on calcareous soil.

In his valuable floristic studies of the vegetation of Lower Saxony, Tüxen (1937) recognizes a variant of the *Salix alba-Populus nigra* association in which *Aegopodium* is one of the most abundant species of the ground flora. This is a streamside woodland community, now usually persisting only in fragments, where dominant woody plants are *Salix alba* and various osiers, with *Populus nigra* and *Alnus glutinosa* also present. The associated species include many strongly nitratophilous plants such as *Humulus, Solanum Dulcamara, Urtica* and *Galium Aparine.*

Tüxen also lists *Aegopodium* as a constituent of several communities of the mesophilous deciduous forests (Fagetalia sylvaticae) and in particular of the mesophilous mixed forests (mesophile Laubmischwälder: Fraxino-Carpinion), dominated by *Quercus Robur* and *Carpinus Betulus* or by *Fraxinus excelsior* and *Acer Pseudoplatanus,* but usually containing *Fagus* as well, and often as an important constituent. Using the nomenclature adopted by Tüxen, *Aegopodium* is a characteristic species (Verbandscharakterart) of the Fraxino-Carpinion and is most prominent on the moister base-rich soils, often calcareous and often gleyed below. It attains its highest constancy and abundance in those forest types which Tüxen regards as the climax communities both on siliceous and on calcareous soils, and is more prominent in Central Germany than in N.W. Germany. These woods are floristically rich, both in woody and in herbaceous species, and include a large majority of the species found in British woods on limestone, chalk and base-rich clays. *Aegopodium* also occurs in woods of the true beech zone, at higher altitudes than the oak-hornbeam and ash woods, but is there no more than an occasional component of the floristically richest types on calcareous soils. (Markgraf, in Rübel, 1932; Diemont, 1938).

In Switzerland, too, *Aegopodium* is found in streamside woods (Alneta incanae) and in oak-hornbeam woods of the mixed deciduous forest belt, but not in those on more definitely acid soils (Stamm, 1938). It occurs also in beechwoods on calcareous substrata: Lüdi (1921) lists it on a steep scree-slope in the Lauterbrunnental at 700-830 m. above sea-level. Here the tree-layer contains *Ulmus glabra, Acer Pseudoplatanus, Fraxinus, Picea* and *Tilia platyphylla* as well as the dominant *Fagus,* and there are rich shrub and herb layers. But it appears to be a more constant component of the mixed *Tilia* woods (Tilieto-Asperuletum taurinae), and especially of those damper types in which *Acer platanoides* is frequent (Trepp, 1947). These are again floristically rich woods on base-rich soils, and the species-list resembles that of the oak-hornbeam and beech woods in which *Aegopodium* occurs, though including in addition a number of warmth-demanding species.

Mixed deciduous forests, with *Quercus Robur, Q. petraea* and *Carpinus* as the most important of a considerable number of tree species, are found throughout the lowlands of Central and Eastern Europe, and *Aegopodium* is a frequent component of their ground-flora. Klika (cited in Stamm, 1938) describes an example of his Querceto-Carpinetum-bohemicum and includes *Aegopodium* amongst the herbs; and the same author (Klika; in Rübel, 1930) records it for three forest communities at Bialowicza, Poland: Carpinetum-typicum, Carpinetum-pinosum, and Quercetum-sessiliflorae. Finally Keller (1927) describes a mixed deciduous forest from the Voronezh District of C. Russia, far beyond

the eastern limits of *Fagus* and *Carpinus,* in which it is a significant constituent.

Aegopodium is often present in *Fagus* and *Fagus-Carpinus* forests of C. Europe, but appears to be more local in them than in the mixed forests of lower altitudes. Domin (in Rübel, 1932) does not mention it at all in his account of beech forests in Czechoslovakia, but von Soó (in Rübel, 1930) gives lists which show it to be a constituent of beech and beech-hornbeam forests throughout the length of the Carpathians, though it is impossible from his paper to get detailed information about its associates and its habitat-preferences. While never more than occasional it attains a frequency (i.e. percentage occurrence in quadrats within the sample areas) ranging from c. 10% to c. 80%, and von Soó includes it in his list of 'Charakterpflanzen des Buchenwaldes in den Karpathen'. It is also included by Stoyanoff (in Rübel, 1932) amongst 'typical and commonest representatives of the herbaceous vegetation' of Bulgarian beech-woods. Markgraf (in Rübel, 1932) and Vierhapper (in Rübel, 1932) also list it for certain beech woods in C. Germany and Austria respectively, Vierhapper classing it as characteristic of the moister beechwoods in which *Fraxinus* is prominent.

This summary makes it clear that *Aegopodium Podagraria* is a natural constituent of deciduous forest on base-rich soils throughout Europe from south Sweden, north-west Germany and Switzerland, eastwards to central Russia, apparently being most prominent in moist Eichenmischwälder and in valley-bottom and stream-side woods, especially in central and eastern Europe. It is also found in beechwoods, and occasionally in coniferous woods.

In north-west Europe, however, *Aegopodium* is by no means confined to forests. Tüxen (1937) includes it in his list of a community characteristic of the sides of streams and ditches on heavy nitrogen-rich soils (*Cirsium oleraceum-Angelica sylvestris* Association, Sub-Association of *Petasites hybridus*). The ecologically most significant species of this community are *Petasites hybridus, Urtica dioica, Anthriscus sylvestris, Dactylis glomerata, Angelica sylvestris, Filipendula Ulmaria, Aegopodium Podagraria* and *Glechoma hederacea.* The same author lists *Aegopodium* as an important constituent of two ruderal communities of the Chenopodietalia medio-europaea, both included in the Arction lappae. One of these, the *Chaerophyllum bulbosum* Association, is found where *Salix alba, Populus nigra,* etc., have been cleared from stream-valleys in country where oak-hornbeam woods form the natural vegetation. Besides *Chaerophyllum bulbosum* and *Aegopodium* other prominent species are *Carduus crispus, Urtica dioica, Artemisia vulgaris, Myosoton aquaticum, Calystegia sepium, Galium Aparine* and *Rumex obtusifolius.* The other is called by Tüxen the *Chenopodium Bonus-Henricus—Urtica urens* Association, and is a strongly nitratophilous and very widespread weed-community in which *Lamium album, Urtica dioica, Plantago*

major, Poa annua, Rumex obtusifolius, Malva neglecta, and *Taraxacum officinale* are other prominent species. These or closely similar communities are known in large parts of Europe, including this country, and it is the frequency with which *Aegopodium* occurs in them that gives it its reputation as being primarily a weed. Its true status has been further obscured by its tendency to bulk largely in the vegetation of woods in which human interference has been considerable. Thus Domin (1928), in a list of species in a *Carpinus-Corylus* wood in the Valley of Radotin, near Prague, divides the ground-flora herbs into 'wood-herbs' and herbs of a weed character, the latter including *Aegopodium, Anthriscus sylvestris, Chaerophyllum temulum, Galium Aparine, Geum urbanum, Campanula rapunculoides, Chelidonium majus* and *Taraxacum officinale.* But there are no good grounds for doubting that *Aegopodium* is a genuine constituent of undisturbed deciduous woodland in many parts of Europe, and the same may well be true of all the species in Domin's list.

In the British Isles *Aegopodium* is an abundant hedgerow plant in the neighbourhood of villages, conspicuous northwards at least to central Scotland; and is too well known as a pernicious weed of gardens and shrubberies, difficult to extirpate because of its numerous and brittle stolons. Not infrequently it becomes prominent in open scrub and streamside swamp-woods near human dwellings, but I have never seen it looking other than secondary in such localities. I have, however, found it in ash-elm woods in the Evenlode valley, in Oxfordshire, on the deep moist colluvial soils at the foot of limestone slopes, and I can see no good reason for doubting that it may be native there. Horwood and Gainsborough, in their *Flora of Leicestershire and Rutland* (1933), write: "As this plant occurs in damp oak wood and in ash oak wood, it may be considered native", and authors of other county floras make similar statements. The similarity of these habitats to some of those in which *Aegopodium* seems undoubtedly native in continental Europe strengthens the case for regarding it as native also in this country. I am informed by Dr. H. Godwin that Miss Allison has found fruits of *Aegopodium* on a Roman site at Cottenham, near Cambridge. The significance of this find is made somewhat doubtful, however, by the fact that *Aegopodium* was long used in various parts of Europe as a green vegetable and as a medicinal plant with a great reputation especially for curing gout. It has certainly been cultivated for these purposes and might have been introduced to the country during the Roman occupation, but its general continental distribution and habitat-preferences seem in favour of the view, put forward here, that it has been a constituent of our native flora at least since the establishment of mixed oak forests in the south.

2. *Chaerophyllum temulum* L.

Chaerophyllum temulum resembles *Aegopodium* in its European distribution but extends less far north, having only a handful

of localities north of 60° N. in Sweden and Finland, and being absent from northern Russia. Nor does it attain the importance of *Aegopodium* as a constituent of woodland floras in central and eastern Europe. Tüxen (1937) includes it in his list for the Fagetum boreo-atlanticum allietosum ursinae, beechwoods on moist calcareous substrata in north-west Germany, its constancy being 12%. It occurs also with about the same constancy in the *Cicerbita alpina* sub-association of Tüxen's Acereto-Fraxinetum, a community in which *Acer Pseudoplatanus, Picea, Fraxinus* and *Fagus* constitute the tree-layer and which occurs on moist slopes in the Harz Mts., in the upper part of the *Fagus* zone. Its rich and luxuriant herb layer resembles that of certain subalpine woods in the mountains of Central Europe. *Chaerophyllum* is also listed for the related streamside ashwoods in the middle and upper *Fagus* zones which Tüxen has named Cariceto remotae—Fraxinetum chrysosplenietosum, though here its constancy is only 5%. It is also a "Charakterart" of Tüxen's Querceto-Carpinetum medioeuropaeum but is a significant constituent only of the moister sub-associations and especially of those beech-hornbeam-oak woods on calcareous or circumneutral soils in which *Aegopodium* also attains its maximal abundance. Markgraf (in Rübel, 1932) records it for two *Mercurialis*-beechwoods in Central Germany, and Domin (in Rübel, 1932) for mixed *Fagus-Acer-Ulmus* woods in the west Carpathians whose chief ground-flora species are *Galeobdolon, Glechoma hirsuta* and *Asperula odorata.* It is rare in Austrian beechwoods, not recorded by Meusel (1935) in the oak and oak-hornbeam woods of the Grabfeld nor by Stamm (1938) in oak-hornbeam woods of Switzerland, listed by Domin (1928) as one of the 'herbs of a weed-character' in a *Carpinus-Corylus* wood near Prague, and by Klika (1930) as a constituent of Carpinetum typicum at Bialowicza in Poland.

The general impression given by these records is that *Chaerophyllum temulum* is a rather unimportant natural constituent chiefly of moist deciduous woods on base-rich substrata, often associated with *Aegopodium* but absent from the drier woods in which that species occurs.

Like *Aegopodium, Chaerophyllum temulum* is conspicuous in certain ruderal and semi-ruderal communities. Tüxen (1937) assigns it a constancy of c. 20% in a widespread community of clearings in moist Querceto-Carpineta, the *Epilobium angustifolium-Senecio sylvaticus* association of the Atropion, sub-association of *Deschampsia caespitosa*; and it is still more prominent in the nitrophilous shade-loving weed-community of hedges, wood-margins, etc., which he terms the Alliario-Chaerophylletum temuli (Tüxen, 1950) and whose most important constituents are *Alliaria, Chaerophyllum temulum, Lapsana communis, Bryonia dioica,* and *Viola odorata.*

In the British Isles *Chaerophyllum temulum* is a plant of hedgerows and wood-margins on better soils through much of the country, though absent from some of the northernmost vice-

counties and much less common in Scotland than *Aegopodium*. It is occasionally found in woods in circumstances suggesting that it may be an original constituent of the ground-flora, but much more generally it is a human associate. I can find no record of its use as a food plant; it has, indeed, been described as poisonous to stock. But it was certainly used medicinally and Hegi (1908-31) states that it was planted in German gardens, apparently for this purpose, around 1560.

Fruits of *Chaerophyllum temulum* have been recorded from interglacial beds at West Wittering, Sussex (Reid, 1899).

3. *Anthriscus sylvestris* (L.) Bernh.

Of the three umbellifers included in this enquiry, *Anthriscus sylvestris* is certainly the most widespread, the most abundant and the one whose original ecological status is the most evident. While *Aegopodium* and *Chaerophyllum temulum* can be regarded as native no further north than Central Sweden, *Anthriscus* extends to the shores of the Arctic Ocean and throughout Scandinavia as a clearly natural constituent of communities which have suffered little or nothing from the hand of man. Important works by Nordhagen (1928, 1943) and Kalela (1939) provide a great deal of information about its rôle in Scandinavian vegetation.

In the mountains of Norway, *Anthriscus sylvestris* is characteristic of the tall-herb communities of base-rich habitats which are grouped by Nordhagen (1943) into his Mulgedion alpini, though it occurs in a wider range of communities at lower levels. The Mulgedia alpini are found either as woodland ground-flora communities, or associated with shrubby willows, or in subalpine meadows with no associated woody plants; and *Anthriscus* occurs in all three situations. It has a constancy of 33% in subalpine birch-woods of *Betula tortuosa* at c. 1020-1100 m. above sea-level in Sikilsdal (Nordhagen, 1943), its chief herbaceous associates being *Aconitum septentrionale, Geranium sylvaticum, Saussurea alpina,* and, more locally, *Mulgedium alpinum* (*Cicerbita alpina*), with *Alchemilla vulgaris* agg., *Angelica sylvestris, Chamaenerion angustifolium, Cirsium heterophyllum, Equisetum pratense, Filipendula Ulmaria, Geum rivale, Gnaphalium norvegicum, Melandrium dioicum, Myosotis sylvatica, Polygonatum verticillatum, Ranunculus acris, Rubus saxatilis, Rumex Acetosa, Solidago Virgaurea, Trientalis europaea* amongst the other herbs present. Further north *Trollius europaeus, Stellaria nemorum,* and *Viola biflora* become important constituents, and *Anthriscus* is more prominent. Birchwoods of this type were seen on mountains in Swedish Lappland, west of Abisko, and the components of the herb layer, including *Anthriscus,* extended above the woods into scrub of *Salix lanata* and other willows, and locally formed subalpine meadows above the willow belt. Kalela (1939) describes 'Hochstaudenwiesen', of essentially the same composition, as characteristic of the more base-rich soils in the 'arctic' zone,

north of the tree-limit, in the Fischer Peninsula of northernmost Finland. They are regarded as truly spontaneous and are developed most typically on steep sunny slopes and on screes and only where the snow melts early. The most demanding of these communities, found on moist calcareous slopes, is dominated by *Anthriscus sylvestris* and *Angelica Archangelica,* with *Geranium sylvaticum, Rumex Acetosa, Stellaria nemorum, Viola biflora, Milium effusum,* and *Trollius europaeus* as other species of high constancy. This is the most productive community of the area, often attaining almost 2 m. in height. Manuring by sea-birds increases its luxuriance locally. *Anthriscus* is also prominent in Kalela's *Geranium sylvaticum*-Wiese (with *Geranium sylvaticum, Viola biflora, Trollius europaeus, Alchemilla vulgaris* agg., *Rumex Acetosa, Chamaenerion angustifolium* and *Filipendula Ulmaria* as species of highest constancy), but less so in other related Hochstaudenwiesen, though fairly well represented in some relativity oligotrophic communities characterized by the abundance of *Athyrium Filix-femina* and *Cicerbita alpina.*

Elsewhere in Europe *Anthriscus* appears to play no very important part in woodland communities, though it is occasionally listed for high level beechwoods on base-rich soils, as by von Soó (1930) for certain woods in the east Carpathians. But it is widespread and locally very abundant in the rich grassland communities (Fettwiesen) which have often replaced forest at all levels from valley-bottoms to the tree limit. These communities fall into two main groups, the Arrhenathereta and Triseteta, characterized by the grasses from which they are named, the latter commonly at higher levels than the former. *Anthriscus* is a conspicuous component of all the types of grassland in which grazing is not very heavy, and especially of those which are mown first and grazed only towards the end of the season: it is most luxuriant where the grassland is dunged.

Apart from these meadows *Anthriscus sylvestris* is also a prominent constituent of the luxuriant stream and ditch-side community which Tüxen names the *'Cirsium oleraceum—Angelica sylvestris* Association, Sub-Association of *Petasites hybridus',* and which has already been mentioned (p. 29) in connection with *Aegopodium.*

In this country *Anthriscus sylvestris* lines our roads and fields over wide areas where the substratum is at least moderately base-rich, becoming a highly characteristic feature of hedgerows in April and May. It invades mowing-grass but is kept down by continuous grazing and so is rarely an important constituent of pastures. It is frequent on the drift-lines of rivers and brackish marshes, but I have so far been unsuccessful in my attempts to find it on those high rocky ledges and terraces, protected from intensive grazing by at least a partial inaccessibility to sheep, where flourish *Trollius, Chamaenerion, Geranium sylvaticum, Rumex Acetosa, Ranunculus acris* and many other late Glacial relicts. I have sought for it in vain on Ben Lawers and neighbouring hills,

on Lochnagar, in Glen Canness and in Caenlochan Glen. I shall be much interested to know whether any readers have seen it in such places, or in mountain birchwoods in Scotland. If it is really absent from such localities, it would be premature to regard it as a Late Glacial survivor, even though its absence might be the result of comparatively recent climatic change. It is perhaps significant that the common form in the north of Great Britain (var. *angustisecta* (Druce)) is somewhat different from the southern form, more glabrescent, with more finely dissected leaves and larger fruit. It is said to extend southwards to Derbyshire, and it is a possible inference that this is the old indigenous form, the southern plant (var. *latisecta* (Druce)) having immigrated at a later date and perhaps through human agency. But further study is required of its morphological distinctness, and of its distribution inside the country and elsewhere, before such speculations can have real value.

Anthriscus sylvestris is eaten by cattle and rabbits and, according to Church (1925) has been used as a pot-herb. It has been recorded from Interglacial beds at West Wittering, Sussex (Reid, 1899).

4. *Tanacetum vulgare* L.

Tansy is a locally important component of the *Geranium sylvaticum*-meadows described by Kalela (1939) from the Fischer Peninsula in northernmost Finland. These occur chiefly on sunny scree and detritus-slopes below cliffs or on stream-banks. *Geranium sylvaticum* and *Trollius europaeus* are the dominant species, and *Chamaenerion angustifolium, Poa nemoralis* and *Anthriscus sylvestris* are conspicuous. *Tanacetum* also occurs in a community dominated by *Chamaenerion* on the sandy bank of the Pummanginjoki river. Here *Deschampsia caespitosa, Rumex Acetosa, Trollius, Ranunculus acris, Alchemilla vulgaris* agg., and *Geranium sylvaticum* are its chief associates.

Further south, *Tanacetum* is listed by Almquist (1929) for several maritime and lake-shore communities in Uppland. It is regarded by him as indigenous in these habitats, and especially on the numerous islets off the coast. Amongst the most interesting of the communities on these 'skerries' are those dominated by *Hippophaë rhamnoides,* of which *Tanacetum* is a frequent and often a prominent constituent. It occurs also in open wind-dwarfed *Juniperus* scrub on moraine with a great variety of associated grasses and herbs. In one such example (Kallskär) the main species were *Juniperus communis, Chamaenerion angustifolium, Origanum vulgare, Festuca ovina* and *F. rubra, Tanacetum vulgare, Agrimonia Eupatoria, Cirsium palustre, Galium verum, Dryopteris Filix-mas* and *D. spinulosa,* with *Cladonia* spp. Yet again, *Tanacetum* is often in Uppland on maritime cliffs. One list (Kalmar; Getberget) includes *Tanacetum* with *Berberis vulgaris, Cotoneaster integerrima, Rosa Afzeliana, Calluna, Artemisia campestris, Asplenium septentrionale, Calamintha Acinos, Clino-*

podium vulgare, Cynanchum vincetoxicum, Geranium sanguineum, Polygonatum officinale, Potentilla argentea, Sedum Telephium, Veronica spicata, Woodsia ilvensis, etc.

These are all communities which have suffered little disturbance from man. *Tanacetum* is also a feature of species-rich maritime grasslands which may owe their freedom from woody plants in part to grazing, though exposure is undoubtedly the chief determining factor and is apparently the only one on some of the smaller islands. These 'maritima örtsbackakr' are commonly tall-growing and their chief constituents are *Arrhenatherum, Avena pubescens, Agrimonia Eupatoria* and *A. odorata, Anthriscus sylvestris, Chamaenerion, Hypericum perforatum, Origanum, Veronica longifolia* and *Tanacetum.*

Lastly, *Tanacetum* is widely spread, in Uppland, in gardens, hedgerows, field-borders, railway-embankments, etc., and is often cultivated, so that it is sometimes difficult or impossible to distinguish between native and secondarily established plants.

Passing southwards from Uppland to north-west Germany, we find that Tüxen (1937) gives *Tanacetum* as a significant component of various drift-line communities by rivers, lakes and the sea. These include a maritime *Atriplex littoralis* association, in which *Atriplex* spp., *Matricaria maritima, Cakile* and *Salsola* are the most constant constituents; and a Bidentetum tripartiti, of riverside flats, characterized by *Atriplex hastata, Chenopodium rubrum, Bidens tripartitus, Rorippa* spp., *Polygonum* spp., *Rumex* spp., etc. It is also recorded as attaining about 30% constancy in two more definitely ruderal communities, the *Chenopodium Bonus-Henricus—Urtica urens* and *Hordeum murinum* associations, the former with *Lamium album, Urtica dioica, Plantago major, Urtica urens, Poa annua, Chenopodium Bonus-Henricus, Rumex obtusifolius* and *Malva neglecta*; the latter with *Hordeum murinum, Capsella Bursa-pastoris, Sisymbrium officinale, Lolium perenne, Polygonum aviculare, Taraxacum officinale,* and *Artemisia vulgaris* as the species of highest constancy.

In a later classification of nitrophilous ruderal communities Tüxen (1950) recognises a Class Artemisietea vulgaris of which *Tanacetum* is one of the characteristic species. The Class consists of perennial nitrophilous herbaceous communities of drift-lines, hedgerows and wood-margins and of waste places throughout the whole of the Eurosiberian region of Europe, excluding only the alpine and subarctic zones. But *Tanacetum* may also attain a fairly high constancy in communities of at least two others of the Classes recognised by Tüxen, the Cakiletea maritimae and the Bidentetea tripartiti, so that it is clearly a conspicuous and very widespread constituent of these nitrophilous assemblages.

Of special interest in this connection is the paper by Nordhagen (1940) on the plant communities of drift-lines in Norway. Brackish lagoons in south Norway have a luxuriant drift-line vegetation which is commonly dominated by *Filipendula Ulmaria,*

though *Euphorbia palustris* or *Festuca pratensis* may dominate where the substratum is stony. *Tanacetum* is often associated both with *Filipendula* and with *Euphorbia palustris.* Nordhagen expresses the view that these drift-lines are ancient and wholly natural habitats and that many common ruderals may well have spread from them when man opened up comparable habitats in and around his settlements. The brackish drift-lines mentioned above support many other species which we now regard as ruderals: *Agropyron repens, Potentilla Anserina, Rumex crispus, Sonchus arvensis, Calystegia sepium, Artemisia vulgaris, Cirsium arvense, Equisetum arvense,* etc.

It may be concluded that *Tanacetum vulgare* is probably a natural component of certain maritime, lake-shore and riverside communities, and especially of drift-lines, throughout much of north-west Europe. It is also a widespread ruderal and has been further favoured by its frequent cultivation.

5. *Tussilago Farfara* L.

Coltsfoot, like Tansy, reaches the extreme north of Scandinavia and is included in Kalela's list (1939) for *Chamaenerion angustifolium* meadows in the Fischer Peninsula, where it is associated with *Anthriscus sylvestris* and *Tanacetum* in a community dominated by *Chamaenerion* and with *Trollius, Geranium sylvaticum, Rumex domesticus, R. Acetosa, Ranunculus acris* and *Solidago Virgaurea.* I have seen it in essentially similar communities in and just above birchwoods near Abisko in Swedish Lappland. But its most characteristic habitats throughout Scandinavia are the calcareous seepage-fens dominated in the north and on mountains by *Saxifraga aizoides, Epilobium alsinifolium* and tufa-forming bryophytes, and in lowland localities in the south by *Juncus subnodulosus.*

In Uppland Almquist (1929) reports *Tussilago* locally on maritime sand and shingle, and as an occasional ground-flora species of certain *Picea* woods on moist base-rich drift soils. Sterner (1938) regards it as probably indigenous in Öland by streamlets (in the forest or otherwise) and on the drift-line amongst boulders. Both these writers record it also in many secondary habitats. Nordhagen (1940) lists it in drift-line vegetation in two localities in south-west Norway, and Hard av Segerstad describes it as native in seepage-fens, by streams and perhaps on the banks of rivers.

Tüxen reports *Tussilago* as occurring in about one in four of the samples of a community characteristic of felled areas in deciduous woodland on heavy calcareous soils in S. Hanover, a variant of the Atropetum belladonnae with abundant *Calamagrostis epigeios*; and, more constantly, in a widespread ruderal community, on similarly heavy base-rich soils, in which *Chenopodium* spp., *Polygonum* spp., *Sonchus* spp., *Senecio vulgaris, Capsella Bursa-pastoris, Equisetum arvense,* and *Ranunculus repens* are prominent.

Turning to this country we find that Gerard (1597) says of coltsfoot that 'This groweth of itselfe neere unto springs and on the brinkes of brookes and rivers, in wet furrows, by ditches sides, and in other moist and waterie places neere unto the sea almost everywhere', and it is not easy to improve on this statement. It is familiar enough as a weed on clays and heavy loams, luxuriating in base-rich and well-manured soils and often becoming a really pernicious weed. But it is also an abundant colonist of boulder-clay banks and cliffs and of drift-line vegetation. And it is frequent at seepage-zones and in the water-washed turf or amongst the boulders by streamlets at all levels to 3,500 ft. or so on our base-rich hills and mountains. I have seen it for instance at seepage-zones between Malham Tarn and Arncliffe and in many spots high up on Ben Lawers and neighbouring hills, and here its native status cannot be doubted.

Coltsfoot, as its Latin name implies, was for long used as a medicinal plant and may occasionally have been planted for that purpose, though we need hardly to suppose that its spread would have been much less than at present had it never been planted. It is of interest that it has been recorded from Post-Glacial beds at Redhall, near Edinburgh (Reid, 1898).

Discussion.

We see, then, that all these five species may very reasonably be regarded as ancient inhabitants of this country. All occur as undoubted natives of neighbouring continental areas, all have been considered as at least probably native in some of their British localities, and for all of them their distribution and habitat-preferences on the European mainland make it a very reasonable inference that they have been in this country since before the beginning of the historical period. For three of them, *Anthriscus, Tanacetum* and *Tussilago,* it seems probable that they became widespread here during the Late Glacial times, since they are constituents of subalpine and near-arctic vegetation in northernmost Scandinavia, though *Anthriscus* may have flourished more particularly in the birchwoods of a slightly later date. The other two, *Aegopodium* and *Chaerophyllum*, are more warmth-demanding and more definitely woodland plants which would not have found optimal conditions until the spread of the mixed oak-forests of late Boreal and Atlantic times. All could have colonised drift-lines and banks by streams, rivers, lakes and the sea-shore, and all would have been available for, and capable of spread into, forest-clearings made by Neolithic and later man. They are all vigorously growing perennials with a strong capacity for vegetative spread, all are nitratophilous and all react in a highly favourable manner to nitrogenous manuring, and so all would become prominent constituents of the vegetation in the vicinity of human settlements. There they would attract attention as potential foods or medicines and might be introduced more widely on that account or unintentionally in carried fodder. Wayside banks and

hedgerows persist to the present time as habitats providing the requisite conditions of base-rich, actively nitrifying soils, often with the light shade, which the three umbellifers seem to favour, and usually with protection from extremes of grazing and trampling to which such tall-growing herbs are susceptible. And, in some localities, drift-lines also persist as relict habitats in which the species have been able to survive.

We have still to consider why the species under consideration have so nearly disappeared from what seem to be their original woodland habitats. The chief factors operating here are clearly the replacement of so large a proportion of woodland on the better types of soil by arable land or grassland, and the mode of management of the residual woodland areas. The British Isles have suffered much heavier losses of their natural woodlands than most other European countries and much of what remains is on the poorer types of soil. Such 'better' woodland as does survive is almost all either coppiced or grazed, both modes of management inimical to tall-growing herbs. It is possible that climatic changes in early historic time have also operated adversely on some of the species. These problems cannot easily be solved until investigations such as those of Dr. Godwin and his collaborators have yielded more positive information about the early history of our British flora and about these hedgerow plants in particular. Meanwhile I can heartily recommend, as a valuable and fascinating study, attempts to elucidate the status of the many other components of our wayside and hedgerow vegetation.

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This paper was discussed as follows:—

MR. MEIKLE stated that he had seen *Anthriscus sylvestris* on mountain cliffs in Ireland. It grows in considerable quantity at about 2000 ft. altitude on the damp cliffs above Lough Muskry in the Galtee Mountains, S. Tipperary. Here it is associated with woodland plants such as *Melandrium dioicum* (L.) Coss. & Germ. and *Orchis mascula* L., montane species such as *Saxifraga stellaris* L., *Oxyria digyna* (L.) Hill, etc., and with *Saxifraga rosacea* Moench and *S. spathularis* Brot.

DR. WATT stated that in Aberdeen coltsfoot was widely used as a substitute for tobacco, and known generally as "Tussilago." He thought it was worthy of note that all five species reviewed by Prof. Clapham favoured habitats which, judging from the associated species, are strongly nitrifying; such associations are likely to be extended by human activities.

PROF. CLAPHAM replied that the strong response of the five species to nitrogen was likely to be responsible for their attracting human attention. Man was likely to find uses for plants brought so prominently to his notice.

DR. DAHL remarked that the best criterion we have that a species is natural in a country and not introduced by man is undoubtedly whether it is established in natural communities. One should be careful, however, not to press this criterion too far. Thus we have historical record of the introduction of *Senecio viscosus* L., but it is nevertheless established in perfectly natural communities along seashores just as well as *Tanacetum vulgare* L. and *Tussilago Farfara* L.

DR. BUTCHER suggested that the two varieties of *Anthriscus sylvestris* which had been mentioned seemed to provide an opportunity for somebody to do some biometrical research.

Following a question from Dr. Walters, DR. DAHL stated that on the introduction of agriculture into Scandinavia, the weeds were apparently recruited from two main natural vegetation types besides those man brought with him. One was the nitrophilous seashore communities, the other the tall herb communities essentially of subalpine, northern and continental types. In the south and west these are replaced by fern communities.

POSSIBLE HUMAN HISTORICAL FACTORS DETERMINING THE DISTRIBUTION OF ERIOPHORUM LATIFOLIUM IN THE NORTH-WEST CONWAY VALLEY

(Exhibit)

R. Elfyn Hughes.

The choice of site for utilisation and occupation by man at any stage in the human settlement of a region is largely determined by:

a. the level of civilisation of the community as reflected in its technical ability.

b. factors that are essentially ecological.

(East (1935), Gradman (1931), Grimes (1945), and Mutton (1938)).

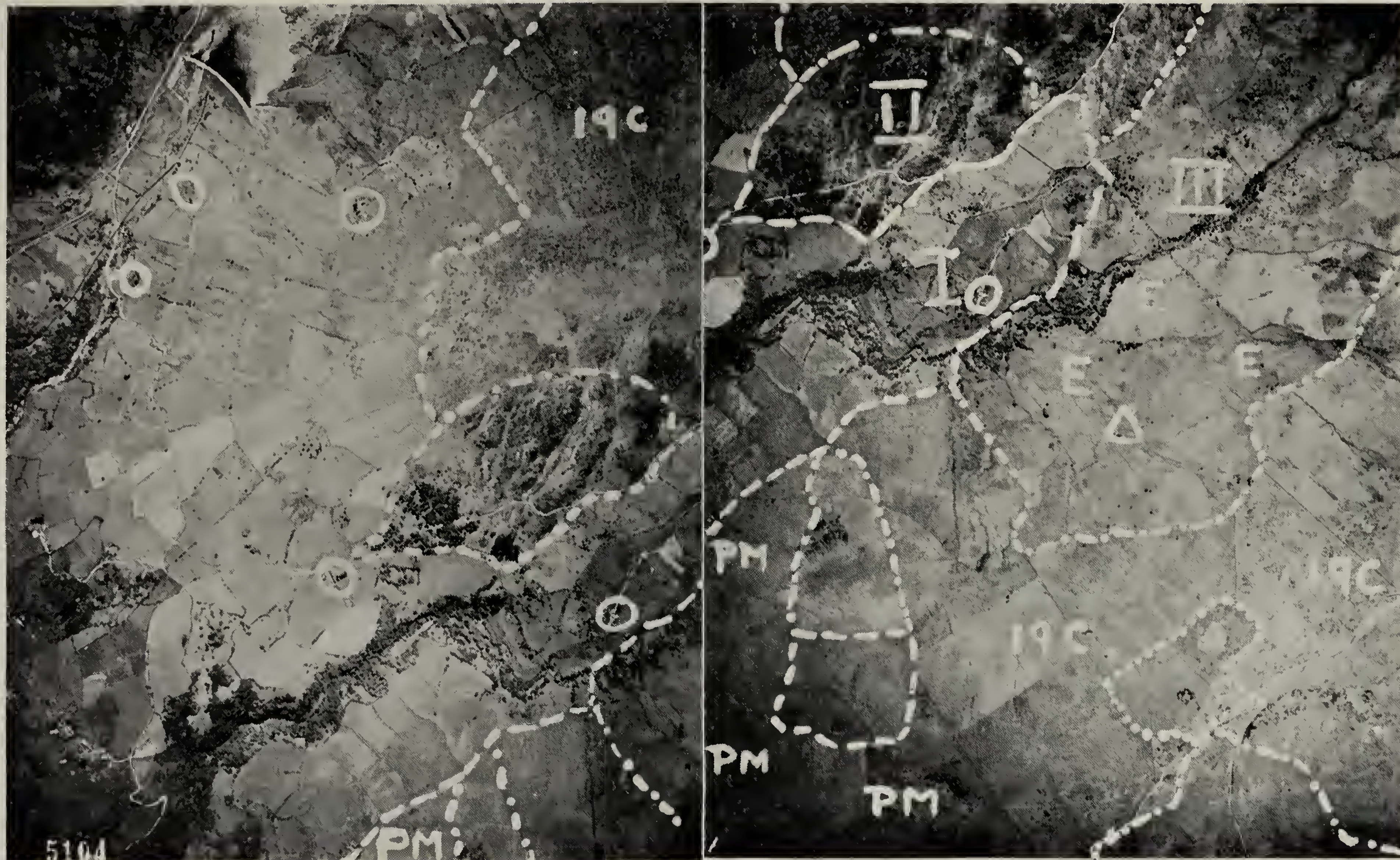
Human settlement has been studied in the north-west Conway Valley (Hughes (1940, 1949b)). It has been shown that terrains characterised by basic igneous rocks (augite dolerite pumice tuffs, and spilitic agglomerates)—occurring either as outcrops or as major constituents of the glacial drifts, have been foci of human settlement at various periods in the past. These terrains are also foci of intense interference with the native vegetation. Within "basic" terrains, local drainage conditions, in particular, have an important influence on site selection by man. The collation of documentary and field evidence shows that, as one would expect, "basic" terrains with a preponderance of free-draining sites at altitudes of 700-1,000 ft. were occupied during the mediaeval period, while extensive areas of impeded drainage were occupied mainly in the 16th century. More difficult country at higher altitude was enclosed or occupied subsequent to the 16th century (sporadic "squatter" movement) and during the 19th century (statutory enclosure).

Soils of impeded drainage, particularly those which are peaty and derived from the "basic" drifts, bear a Molinietum of eutrophic affinities[1], of subseral origin from upland alderwood. (The floristic composition of the community is given in Table I).

Eriophorum latifolium, a species atypical of western Britain, is present sporadically in this community in the Conway Valley. The peats on which it occurs are moderately acid, and of a high nutrient status (table II). These soils are discussed in greater detail elsewhere (Hughes (1949a))—and have affinities with fen peat. This cotton grass appears to be sensitive to anthropogenic influences. Therefore, since it occurs within "basic" terrains, the foci of major human interference at different periods in history—

[1] The central group of species within the community are primarily eutrophic though some other species reflect a tendency to oligotrophism (e.g., *Sphagnum* spp. and *Eriophorum angustifolium*).

PLATE I.



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Valley A. Valley B.

Human Settlements of Valleys A and B.

For key, see p. 45.

PLATE II.

Royal Air Force. Crown Copyright reserved.

Human Settlement of Valley C.

For key, see p. 45.

the study of its distribution and ecology in the Conway Valley provides tentative evidence of the influence of past and contemporary anthropogenic factors on the distribution of a species.

On edaphic grounds the potential distribution of *E. latifolium* in the Conway Valley is greater than at present. Thus, potential habitats for the species are found in three major lateral valleys, A. (Porth llwyd), B. (Dulyn) and C. (south branch of Tafolog), but it is not found in A. The soils of the three valleys are of similar origin, being derived from "basic" drifts, but they differ in the general features of their topography, such that the prevalence of soils of free drainage is in the following order: A>C>B. Documentary evidence shows that valley A was extensively occupied in the mediaeval period; C, to a limited extent during the mediaeval period, while the major part of it was enclosed and occupied in the 16th century with extensions to higher altitudes in subsequent centuries. In valley B, major occupation occurred in the 16th century with marginal earlier occupation, with post-16th century expension at higher altitudes.

The present-day intensity of summer grazing shows the same trend. Much of valley A will carry up to 5 ewe units to the acre, valley C is variable, with local areas carrying 5 (free draining soils) and others about 1.5 (wetter soils) ewe units to the acre.[2] Valley B carries about 1.5 ewe units to the acre. It is, therefore, evident that since mediaeval times anthropogenic influences have been greater in A than in C and in C than B. It is tentatively suggested that this has an important bearing on the present-day distribution of *E. latifolium* in the three valleys. This species is absent in the eutrophic Molinietum of valley A, because it has been subject to intense anthropogenic influences from the mediaeval period—this continues to-day in the form of heavy grazing. On the other hand in valley B, *E. latifolium* occurs extensively, since it was occupied at a later period (16th century), subject to less intense settlement, and a lower grazing intensity to-day.

Valley C occupies an intermediate position, as it was partly occupied in the mediaeval period and partly in the 16th century, and present-day intensity of grazing is variable, so that *E. latifolium* is of limited occurrence, though its potential range is greater. The relevant details are set out in the aerial photographs (Plates I and II) and below.

Valley A (*Porth llwyd*).

The extensive human settlement of the valley is clearly evident in the photograph, and sites of mediaeval occupation are prevalent. Early settlement here is primarily due to the prevalence of soils of free drainage. Eutrophic Molinietum occurs

[2] Grazing intensity of all livestock is expressed in terms of a common ewe unit (vide Watson & Moore; 1949, *Agriculture: The Science and Practice of British Farming*, p. 795; London).

in small hollows and along seepage lines, and is distinctly more anthropogenic than its equivalent in the other two valleys—i.e. the *Molinia* is shorter and more closely grazed (5 ewe units/acre), and there is a greater prevalence of *Holcus lanatus* and *Ranunculus acris.* Note the absence of *E. latifolium* sites.

Valley B (Dulyn).

The pre-mediaeval phase of settlement bears no relationship to the problem discussed here; details are presented elsewhere (Hughes (1940)). Major mediaeval settlement is confined to the south side of the valley—selecting outcrops of basic igneous rocks (I). Note the 16th century spread to acidic terrain (rhyolite) with a heath vegetation (II) and to glacial drift with impeded drainage (III) bearing an eutrophic Molinietum. The north side of the valley was occupied mainly in the 16th century. Here peaty soils abound, and bear an eutrophic Molinietum in which *E. latifolium* is frequent.[3] The *Molinia* here is less heavily grazed (intensity 1.5 ewe units/acre) and is taller than in valley A. Here grazing intensity appears to be the optimum for the survival of *E. latifolium.* Any change in land utilisation leading to heavier stocking in summer, or a change in drainage conditions, would probably lead to the partial or total elimination of this species.

Valley C.

Here we have more intensive mediaeval occupation than in valley B. Note the occurrence of *E. latifolium* within an area of 16th century enclosure, and where grazing intensity has remained comparatively low (1.5 ewe units/acre). High level 16th century occupation has occurred in relation to the prevalence of basic igneous rocks on the flanks of Peny Gader (I).

Post 16th century ("squatter" movement) and 19th century enclosure (II) occur at higher altitudes, and at lower altitudes on parts of the glacial drift which bears a Nardetum (gley podsolic soils) (III).

Conclusions.

The most important factors which determine the presence of *E. latifolium* in the Conway Valley are primarily edaphic—these depending on the presence of basic igneous rocks in the district. Its distribution with the eutrophic Molinietum in which it occurs, appears to be dependent on past and present-day intensity of anthropogenic factors. The Molinietum of areas occupied in the mediaeval period, and still heavily grazed, bear no *E. latifolium.* But areas occupied initially in the 16th century and but lightly grazed, harbour abundant *E. latifolium.* The importance of these considerations in the conservation of the species is stressed.

[3] This side of the valley was described as alderwood in the 16th century.

TABLE I.

FLORISTIC COMPOSITION OF THE EUTROPIC MOLINIETUM.

(Number of sites studied =41).

Constancy 5

Molinia caerulea a. to co-d.
Juncus acutiflorus a. to co-d.
Agrostis sp. f. la.

Constancy 4

Holcus lanatus f. la.
Anthoxanthum odoratum f.
Festuca rubra f.
Festuca ovina o.
Potentilla erecta o. f. lf.
Carex panicea f. la.
Succisa pratensis f.
Narthecium ossifragum o. lf.
Sphagnum sp. f. la.

Constancy 3

Briza media o. f. la.
Lotus uliginosus o. f. lf.
Carex echinata f.
Luzula multiflora var. *congesta* o. f.

Those species in the lower constancy groups include species of—

non-acid peat species, e.g. *Eriophorum latifolium* (2. o. la.)
Schoenus nigricans (1. lf.)

acid peats, e.g. *Eriophorum angustifolium* (2. o. la.)
Trichophorum caespitosum (1. lo.)
Juncus squarrosus (1. lo.)
Nardus stricta (2. o.)

wet soils generally, e.g., *Cirsium palustre* (2. o.)
Hydrocotyle vulgaris (2. o.)
Achillea ptarmica (1. lo.)

heath, e.g. *Vaccinium Myrtillus* (1. lo.)
Ulex Gallii (1. lo.)

non-exacting species of agricultural grassland, e.g.
Cynosurus cristatus (2. o. lo. f.)
Plantago lanceolata (1. lo.)
Luzula campestris (1. lo.)

exacting species of agricultural grassland, e.g.
Trifolium repens (2. o.)
Trifolium pratense (1. lo.)
Poa trivialis (1. lo.)

(The numbers in the list refer to the constancy groups of the species referred to.)

Table II.
Environment of the Eutrophic Molinietum.

Altitude	Community—500-1100 ft. O.D. *E. latifolium*—900-1000 ft.
Rainfall	60-70″ per annum
Soil	permanently wet, deep peat (depth at least 1′ 6″) pH—5 to 6.5

The following are analytical data for two sites in which *E. latifolium* occurs.

	pH	Exch. CaO %	Available P_2O_5 %	Exch. K_20 %
Valley A.				
0-8″ Dark peaty material	6.20	0.8	0.0291	0.255
Valley B.				
0-6″ Dark peaty material	5.28	1.72	0.0045	0.235
6″ + Light Brown peaty	5.41	1.28	0.0059	0.320

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The following sources have been used in determining the pattern of human settlement in the Conway Valley.

1. Ministers' Accounts for Wales in the Public Record Office for the 13th and 14th century.
2. *The Record of Caernarvon 1352.*
3. *The Account of Bartholomew of Bolde.* Bangor MS. 1939 (Circa 1400).
4. Jones-Pierce T. The Gafael in Bangor Manuscript 1939, *Trans. Hon. Soc. Cymrodorion*, **1942**, 158-188.
5. Various Manuscripts in the Baron Hill and Vaynol Papers, housed at the University College of N. Wales, Bangor. The former papers cover a period from the late 14th century to the present-day.

A detailed statement of the material used will appear in a later paper in the *Journal of Ecology.*

Key to Aerial Photographs

(Published by kind permission of the Air Ministry).

Pre-mediaeval occupation **P M**
Mediaeval limits of land occupation ▬ ▬ ▬
Mediaeval sites of habitation **O**
Sixteenth century limits of land enclosure ▬ • ▬
Sixteenth century sites of habitation △
Post-sixteenth century "squatter" enclosures and sites of habitation • • • •
Nineteenth century enclosures are indicated as **19 C**
The sites of *Eriophorum latifolium* **E**

SOME RECENT MODIFICATIONS IN THE FLORA AND THE VEGETATION OF THE VALOIS

PAUL JOVET (Paris).

(The following paper was delivered by Dr. Paul Jovet of the Muséum National d'Histoire Naturelle, Paris, in French. It was so clearly enunciated that most of those present had no difficulty in following the theme, but it is thought preferable to publish this translation kindly prepared by Mrs. A. N. Gibby. The scientific names are those in current use in France and in some cases differ from those familiar in this country.—EDITOR.)

The flora and vegetation of the Valois country, situated to the north and north-east of Paris, have been the subject of a recent publication.[1] When comparing the daily observations made by the Abbé Questier between the years 1843 and 1876 with those made by other botanists, as well as myself (from 1924 to 1949), one notes the disappearance of certain species, the substitution of one species for another, new introductions and the creation of new stations. An attempt will be made to deal briefly with several of these modifications.

Disappearance:—*Lycopodium Selago* was destroyed in a landslide immediately after its discovery. Rare Hepatics have disappeared as a result of the quarrying of siliceous sandstone. The tapping of springs has destroyed stations for Alneta-Sphagneta and *Zannichellia.* The clearing of the surroundings of ponds has eradicated *Littorella uniflora* and *Limosella aquatica* and *Botrychium Lunaria,* already rather rare during the last century, has not been found again. Fires on calcareous slopes have eliminated *Bunium Bulbocastanum* and certain orchids. Walkers and campers are responsible for the diminution of *Phleum arenarium* and *Pulsatilla vulgaris* and the disappearance of *Herminium monorchis.* Through the scraping of a wall *Cystopteris fragilis* has never re-appeared. Houses have been built over woods of *Quercus lanuginosa* (*Q. pubescens*) with associated *Thalictrum minus, Inula hirta* and *Gentiana cruciata.* Collectors have exterminated *Ranunculus Questieri* and *Antennaria dioica.*

Substitutions:—Siliceous pastures, where Questier used to collect *Myosurus minimus, Delia segetalis, Gypsophila muralis,* etc., have been drained and their character altered by the application of lime; now, plants are to be found which are either indifferent as to soil or slightly calcicole The cleaning of seeds has resulted in the very considerable reduction in the occurrence of

[1]Jovet, P., 1949. *Le Valois—Phytosociologie et Phytogéographie.* See review by J. E. Lousley in 1951, *Watsonia,* **2**, 143-144.

Caucalis daucoides (*C. lappula*) and *Lolium temulentum*. Man has removed *Daphne Mezereum, D. Laureola* and *Anemone Hepatica* to transfer them to parks made in Querceta-Fraxineta. Forest paths, now too well cared for, have lost many species such as *Equisetum sylvaticum, Alchemilla vulgaris,* but *Agrimonia odorata* and *Juncus tenuis* have become very common. Silicicole oak assemblages have been replaced by woods of *Pinus sylvestris* and *Abies alba,* where *Goodyera repens* and *Monotropa hypophegea* are not rare (Questier did not come across these).

In cultivated fields Questier saw *Veronica persica* once only at the end of his life; this species has now spread everywhere. At present *Amaranthus Bouchoni* and *Chenopodium striatum* are replacing *Amaranthus retroflexus* and *Chenopodium album.* Recently *Galinsoga parviflora* has invaded beetroot fields in the Aisne Département. On podsolic soil (with *Erica tetralix*), which has already been greatly altered by the digging of peat holes, poplars are to be planted. Foresters greatly change many Alneta-Sphagneta, so that two species of *Drosera* have disappeared, as has *Osmunda regalis* from most of such localities; they accelerate the normal process of evolution by planting trees in clearings and are responsible for the loss of *Campanula persicifolia* and *Filipendula vulgaris* (*F. hexapetala*).

About 1860, Questier noted the first plantations of poplars; now all the valleys have become poplar forests; meadows where *Schoenus nigricans, Juncus obtusiflorus* (*J. subnodulosus*) and *Gentiana pneumonanthe* and *Liparis Loeselii* used to be found hardly exist now. The removal of peat has left large trenches filled with water which are being populated by *Chara* and the larger species of *Hypnaceae.* Thus evolution is starting afresh. *Swertia perennis* has become rather rare and *Carex dioica* and *Senecio spathulifolius* are no longer to be found.

Volumes could be written concerning biotic factors, inter-competition among plants resulting in the extermination of *Dentaria pinnata,* fungal diseases, the activities of rabbits, deer, boars, birds, insects, etc.

Creation of new habitats:—Questier saw about 1860 the first excavations for the railway lines; embankments, strengthened by calcareous stones, have created very favourable stations for small bryophytes, especially *Southbya nigrella, Cephaloziella Baumgartneri,* and so the extension of these has been greatly helped. Calcareous slopes in the open have been populated with *Bromus erectus, Galium glaucum* (*Asperula galioides*), *Lathyrus latifolius* and *Poterium muricatum,* species unknown to Questier.

In the neighbourhood of large sugar refineries, *Chenopodium glaucum, C. ficifolium* and *C. rubrum* have appeared. The banks of the rivers Oise and Ourcq have been reinforced in places by calcareous walls, and now mosses such as *Cinclidotus riparius, C. fontinaloides* and *Fissidens crassipes* are plentiful, where they could not live formerly on the earthy banks.

Agropyron glaucum, now frequently found along the Oise, is not mentioned by Questier, nor the following plants which are to be seen along railway lines:—*Erucastrum gallicum, Salvia verticillata, Eragrostis minor* and the very common *Senecio viscosus.* He knew *Linaria repens* (*L. striata*) in but one station; now it has been spread by the railway. Several secondary railway lines are now disused and some of these species will eventually disappear. On the sides of roads *Euphorbia Esula* is often seen and the great extension of *Matricaria discoidea* (*M. matricarioides*) came about after the 1914-18 War; now it is to be found on roads everywhere.

Yet other species, unknown in the Valois in Questier's time, notably *Coronilla varia* and many cultivated garden plants, have become naturalised, e.g. several species of *Aster, Solidago Virgaurea* and *S. glabra,* and, recently, *Buddleja variabilis* has greatly tended its range.

In his parish of Thury-en-Valois Questier saw *Prunus Padus* planted in large numbers for the purpose of re-introducing trees on land occupied by heaths. Since then, *P. Padus* has been introduced into parks and gardens, but birds have caused its spread into numerous valleys. Similarly *Alnus incana,* planted in peaty valleys and also on certain calcareous slopes, has become fairly common, but its hybrid with *A. glutinosa* remains a scarce plant.

If *Acer Pseudo-platanus* is planted here and there in forests, it assumes the appearance of being spontaneous in the east of the Valois; it is often introduced in parks and gardens and along road verges; its seeds germinate very readily on waste ground, among ruins, wood-sides, etc., and everywhere it is naturalised with great ease. Thus we find here three woody mid-European species which are extending more and more from east to west.

Conclusions:—During the past century many localities in the Valois have been greatly altered by the creation of meadow land, the bringing of land under cultivation (with the resulting disappearance of *Lycopodium clavatum*), the building of houses, the construction of railways (and now the disuse of some of them), the quarrying of rocks, the excessive collecting of the rarest plants, numerous plantations of trees (poplars, coniferous trees, American oaks, *Robinia pseudo-acacia*), the maintenance of paths, drainage, etc. However, a fairly large number of localities noted by Questier have been re-discovered. Many new stations have been brought into being. If most of the plants introduced by man, voluntarily or otherwise, thrive in artificial stations, others have established themselves in habitats which are semi-natural or hardly altered; they really now form a part of the present flora of the Valois.

RECENT ADDITIONS TO THE BRITISH FLORA
(Exhibit)

R. D. Meikle.

Those who consider the British flora completely known and worked out will be surprised, I am sure, to learn that the list of post-war additions is so long that I have been compelled, for reasons of time and space, to limit my paper to but a fraction of the total. It has been difficult to know how and where to make the cuts, but two groups I almost immediately excluded—aliens and microspecies—the first because they are coming and going in an endless stream, occasionally leaving a mark on our landscape, as in the case of *Senecio squalidus,* but more often mere waifs and strays left to perish on a dunghill. Of the making of many microspecies there is, seemingly, no end, and I am afraid I find at times that much study of them, or many of them, is, as with books, a weariness of the flesh. If I were to include all the more recently discovered *Hieracia,* Orchids, Euphrasias, *Rubi* and the like, I am afraid my list would never end. Of the remaining groups, one has been excluded through want of personal knowledge—*Potamogeton epihydrus,* a very interesting addition to the American element of our flora, recently identified by Prof. Heslop-Harrison from material which he collected in the Outer Hebrides.

Two Irish finds, *Orchis cruenta* and *Orchis Traunsteineri,* which I have exhibited, are plants for the specialist, and I am not competent to discuss them. *Nasturtium microphyllum* is by now sufficiently well known to you all to require no further discussion. *Homogyne alpina, Agropyron Donianum* and *Milium scabrum* are not really discoveries, but interesting re-discoveries confirming old records, not strictly within the scope of my exhibit.

Patriotism moves me to add that three interesting plants, *Hierochloë odorata,* the Holy Grass, *Cirsium heterophyllum,* the Melancholy Thistle and *Scheuchzeria palustris* have recently been recorded for the first time from Ireland, but, compared with England, Scotland and Wales, Ireland is, for a great part, scarcely known botanically, and additions to the Irish flora are likely to be numerous as botanical investigation proceeds.

Having dispensed briefly with the above, four plants, all Linneons, remain for more detailed consideration—two of them species new to the British Flora, two new genera and one also a new family—they are: *Diapensia lapponica,* first collected by Mr. C. F. Tebbutt near Fort William in Inverness-shire on July 5th 1951, and identified at Kew by Mr. R. A. Blakelock, who has since published a preliminary note on the discovery in the *Kew Bulletin* for 1951, page 325. Subsequent search has shown that *Diapensia* is relatively plentiful in the area where it was first found, and un-

doubtedly native there. It may yet be found elsewhere in W. Scotland, though it is strange that a plant, so conspicuous when in flower, should have escaped attention for so long, unless very rare and local. The Scottish plants have not yet been seen in flower, and it is hoped that further notes on the plant will be published when information is available.

Diapensia lapponica (belonging to the family *Diapensiaceae,* new to the British Flora) has a circumarctic distribution, the var. *lapponica* (which includes the Scottish plant) occurring in Eastern N. America, Greenland, Iceland, Norway, Sweden, Finland, Russia and N. W. Siberia, the var. *obovata* in Western N. America, Kamchatka, and N. E. Siberia.

Diapensia was discovered, not by a botanist, but by an ornithologist, in an area which many botanists considered "worked-out" or too dull to be worth a visit. The moral is obvious, and one can only hope that Mr. Tebbutt's find will lead others to re-examine unpromising ground and give Clova and Lawers a rest.

Koenigia islandica is one of the few British plants to have been first discovered in an herbarium. Specimens collected by Mr. H. M. Montford and Dr. Montford near the summit of the Storr on the Isle of Skye, on the 31st August 1934, and erroneously labelled *Peplis,* were found by Mr. B. L. Burtt in the Kew herbarium in 1950. Since that date Mr. J. E. Raven has re-found the plant in several localities and in considerable quantity in Skye, and suggests that *Koenigia* may be found elsewhere in Scotland. It is an inconspicuous herb, readily passed by as *Montia* or *Peplis* but quite distinct on closer examination, the nutlets are trigonous and typical of *Polygonaceae. Koenigia,* according to Mr. Raven, will grow in a variety of habitats, providing it is free from competition with more vigorous species. It is generally associated with plants such as *Cherleria, Salix herbacea, Juncus triglumis, Sibbaldia, Arabis petraea* and other common northern or montane species.

Like *Diapensia,* it has a circumarctic distribution, occurring in both the Old and the New Worlds, but extends further south than *Diapensia,* to Tibet and Kashmir, and has been reported from Tierra del Fuego in southernmost America, though this record may refer to a closely allied species.

Equisetum ramosissimum. A full account of this interesting discovery has been published by Mr. A. H. G. Alston in *Watsonia* (1949). The Horsetail occurs along a limited stretch of river-bank near Boston, Lincolnshire, growing amongst long grass. It was first seen by Mr. H. K. Airy Shaw in July 1947.

Although related to *Equisetum hyemale* and *E. Moorei, Equisetum ramosissimum* differs from both of these in bearing a considerable number of lax, slender branches, and looks, at first sight, rather more like the hybrid *Equisetum litorale,* though the rough stems and apiculate cones show that it belongs to the subgenus *Hippochaete.*

Equisetum ramosissimum has a very wide distribution, scattered here and there throughout Eurasia, and in temperate and tropical Africa. In Europe it occurs chiefly in the Mediterranean area and in Southern Germany, but it has outposts in Brittany, Holland and the Rhine Valley, so that the British station is not altogether outside the range of its natural distribution. Horsetails are rarely recorded as aliens, and it is most unlikely that *Equisetum ramosissimum* should have been deliberately planted at Boston. Perhaps, as with the Oak and Parsley Ferns in Ireland, the Lincolnshire colony of *Equisetum ramosissimum* has developed recently from wind-borne spores carried westwards from the Continent. On the other hand, investigation may show that the plant is more widespread in the area than present records suggest.

Cerastium brachypetalum was discovered by Mr. E. Milne-Redhead on May 18th 1947 on the bank of a railway cutting in Bedfordshire, between Sharnbrook and Irchester. All the British material collected has been referred to the variety *eglandulosum* of Fenzl, which lacks the glandular hairs of the type. *Cerastium brachypetalum* is widespread in Europe, extending from Southern Scandinavia to the Mediterranean, and from Spain eastwards to the Caucasus. It is also recorded from North Africa, but is apparently absent from the North coast of France. The var. *eglandulosum* is essentially a plant of Central Europe, so that from habitat and knowledge of its extra-British distribution, it seems likely that *Cerastium brachypetalum* is a comparatively recent arrival. Further search may yet show that the Bedfordshire railway-side colony is, in fact, derived from native British stock growing in a natural habitat, for, to the uninitiated, *Cerastium brachypetalum* might easily be passed by as a form of the common *Cerastium viscosum,* though the dense silvery indumentum of stems and leaves gives it a distinctive look.

The species was included by Salmon in the lists of plants he considered likely to be found in Britain, and I am giving it special mention to-day in the hope that it may be discovered elsewhere. A good description of *Cerastium brachypetalum* and a key to the British *Cerastia* was published by Mr. Milne-Redhead in *The Naturalist,* 1947, pp. 95, 96.

Canon Raven remarked that during 1951 he had painted three new and important British plants from fresh material.

Mr. Milne-Redhead said that since he had published his paper on *Cerastium brachypetalum,* his attention had been drawn to its occurrence in Holland and Belgium and these countries should be added to the distribution given.

A ZOOLOGIST'S APPROACH TO A CHANGING FLORA

Dr. Maurice Burton.

The Royal Parks Committee on Bird Sanctuaries has repeatedly expressed the opinion that where an undergrowth, particularly of bramble, is allowed to grow, small song-birds are encouraged to take up residence, and to nest, to a greater extent than where only thickets of rhododendrons are available. This is a sufficiently striking instance of the zoologists' awareness of the effect on animal populations of a change in the flora. Again, the numbers of mistle thrushes have increased and the cause is believed to be the increased supply of food derived from the fruits of ornamental shrubs and trees.

It is natural, in this heyday of ornithology, that our two first examples should be concerned with birds. Nevertheless, they illustrate the two main impacts on animals generally of changes in the flora: through the food-supply, and the provision or withholding of shelter.

A third example illustrates a further principle, the relative adaptability of animals. In the course of human settlement there is a radical reduction in the number of old and rotten trees. Woodpeckers nest in such trees; also they obtain their sustenance from the insect grubs assisting the dissolution of the wood. It has been suggested that, as a result of the reduction in number of suitably old trees, the green woodpecker may have become largely a ground feeder, digging for ants and possibly other things in the soil.

Adaptability in the matter of food is expressed, however, in a natural catholicity in diet, so that the loss of one thing as the main article of food is counter-balanced by the adoption of another. The green woodpecker's menu, for example, as taken from the *Handbook of British Birds* is: "chiefly larvae of wood-boring insects and ants; cases of serious damage to bees and hives also recorded. In one case 50-60 millipedes found in one stomach; remains of a bird's egg also once occurred and worms eaten. Vegetable matter also eaten, acorns, pine-seeds, oats, *Pyracantha* berries, cherries and apples recorded".

The complete carnivore or herbivore is very rare. Among mammals the most striking exception is the koala, the Australian Teddy Bear, which takes nothing but eucalyptus leaves. Moreover, leaves at the wrong stage of growth are said to be lethal. Such dependence upon a single food-plant is very rare. It still does not prove, however, that the koala is one hundred per cent. vegetarian. Whether it takes animal protein—say insects—incidentally, and whether such protein is essential to it is not known. A typical herbivore such as a cow probably takes in a

fair amount of animal protein from invertebrates living on the grass; even the giant panda, with its main diet of bamboo shoots, is known to eat fish and small mammals in its wild state. On the other hand, such a typical carnivore as a lion is known to seek out a particular bulb and eat it, and to take fruits fallen from a wild plum-tree.

In any survey of the effects of a changing flora, it is necessary to keep food chains in mind. The lower invertebrates need detain us hardly at all, for apart from the Protozoa, whose linkage with the flora is somewhat obscure, the invertebrates on the land are mainly earthworms, dependent upon vegetation after it is broken down, and the mollusca, that seem capable of eating anything—living or dead vegetation, each other, the label of a matchbox, paper, and so on. In other words, both are supremely independent of changes in the flora. Even the mollusca, such as the Clausilias we normally associate with beech woods, seem to be able quite readily to transfer to another environment if the need arise.

In insects, we have, however, another situation. First of all, their study is important because they are so numerous. Their species, probably number more than a million throughout the world, so that they represent a high percentage—probably three-quarters—of the animal kingdom. In populations they are as countless as the sands of the sea-shore. They afford the main and direct subsistence for many fishes (e.g. mayfly, caddis and so on), all our frogs, toads and lizards, many species of birds and not a few of our mammals, especially when bats are taken into account. Indirectly, by nourishing these, which are eaten by other animals higher in the food chains, insects can be said to support the many birds of prey and of predatory mammals. If we count also the berry and fruit feeders among birds and mammals, insects acting as pollinators form a factor by no means negligible.

If anywhere in our native fauna we should expect to find animals narrowly linked with a food plant, and therefore occupying a precarious position in relation to potential changes in the flora, it is among insects. The very names of many of them suggest this. Examination shows, however, that to a large extent even this is delusory. We speak of the privet hawk moth, and imagine that its sole food is the foliage of privet. Yet its larvae will feed equally well on lilac, laurustinus, guelder rose, holly and ash, and to a lesser extent on willow, dogwood, hop, snowberry, rowan, wayfaring tree, evergreen oak, forsythia and others. The larva of the cabbage white butterfly, despite its name, will feed on a great variety of *Cruciferae*. It is true that others are more restricted. The poplar hawk moth, so far as is known, takes only poplar and *Salix*. The pine hawk moth is restricted to Scots pine and Norway spruce. The convolvulus hawk moth lives on either the lesser or the greater bindweed. Many species seem to live exclusively on oak, others exclusively

on birch or beech. On the other hand, it has frequently been found that captive larvae will take foliage of species other than those eaten in a wild state, and it must remain an open question, whether the linkage with a particular food plant is as close as is sometimes supposed.

Another possible line of enquiry to be correlated with changes in the flora relates to the fact that some insects prey on a different food plant at different stages, even of the larval life. And it could happen that the mere upsetting of a plant association—removing an essential plant link—might be disastrous to a particular species of insect even though the remaining species of plants were unaffected.

But food is not the only, or even the major consideration. Two other factors must be considered. The first is shelter, and the second is the innate behaviour at pupation. A caterpillar used to feeding and pupating inside a bullrush may be quite well able to feed on another plant whose stems are not sufficiently great in diameter to give it shelter. But this question of shelter leads to an even more important aspect of our survey. The caterpillars of the wainscot moths have a very elaborate behaviour pattern. They bore through the stem of the rush and, after having made an entry plug the hole with detritus. One of them travels up the interior of the stem and, having ascended a certain distance, turns about so that it is head downwards. Then, just before pupating, it spins a web of silk across the lumen of the rush, the purpose of which is to keep the pupa from slipping down. There is, however, yet another link. Before ascending, the larva prepares the exit for the moth-to-come. Just below its own point of entry into the rush it eats away the wall of the stem outwards as far as the cuticle, leaving as it were a circular exit covered with a tympanum. When the moth emerges from the pupal case, it has only to brush aside the silken web, crawl down the stem and rupture the tympanum, to make its entry upon the world.

It is axiomatic that, in a chain of instinctive behaviour, each succeeding action is touched off by the performance of the one preceding it. If for any reason an one action of the chain cannot be carried out the whole sequence breaks down. An example of the deep-rooted nature of instinctive behaviour is seen in the Cynthia moth, which pupates on a leaf, the caterpillar spinning a silken cocoon and drawing the leaf around the cocoon. To prevent the deciduous leaf falling, the silk of the cocoon is carried along the petiole and round the stalk. A Cynthia caterpillar placed in a box just before pupation will spin a cocoon of silk and will carry the silk along an imaginary petiole and round an imaginary stem.

To return to the wainscot moth, if compelled to feed on something other than the bullrush, probably everything would be all right until the time for pupation drew near. Presumably, then, the absence of any one of the many normal factors can serve to deflect the working out of the instinctive chain. The lumen of the plant stem may be too large or too small, the wall of the stem too

thin or too thick and so on. In a highly specialised species there is no margin for adjustment and presumably the chain would break down.

Insects, then, are likely to suffer from one or other of the following if a change occurs in the flora: (1) from inability to change to a new food-plant; (2) from purely mechanical causes, such as inadequate shelter; (3) from upsets in the chain of instinctive behaviour at pupation; (4) and from an ecological conservatism.

It is convenient to use the terms euryplastic and stenoplastic, to describe organisms that are tolerant of a wide variety of environment and those tied to a narrow environment. In considering these, much more than food and shelter, or even chains of instinct, are involved. Relative humidity will depend upon vegetation and particularly upon forest growths, so will the amount of illumination, the temperature and so on. The spread of agriculture encourages certain species of insects at the expense of others, and such changes are most evident in the great increase in their populations. As a result, insectivorous birds increase in the cultivated areas. But then, other factors come in to confuse the picture. At the same time as these things are happening raptorial birds decrease, partly through persecution and partly through the destruction of trees, and with them their nesting sites. Then again, so long as hedges are cultivated the passerine birds are encouraged. When they are cut down, shelter is lost and the passerines suffer. With the spread of agriculture the oaks are reduced in numbers, and jays that are so largely acorn-eaters suffer, or they turn to robbing nests or killing small birds. The use of artificial fertilizers, and especially the cult of the clean stable, reduces manure heaps and the litter and untidiness of the old-time farmstead goes, and with it the insects associated with animal ordure. These are mainly dipterous flies and with their loss comes a diminution in swifts, swallows and martins. The interests of the farmer demands—or so it is usually thought—the destruction of the carnivorous mammals, stoats, weasels, martens, badgers, foxes, and, in turn, the rabbit, rat and mouse enjoy a heyday. All such changes are, however, of greater or lesser degree according to whether the species is euryplastic, like the rat, or stenoplastic, like the jay.

There is yet another heading under which changes in a flora might conceivably affect a fauna, perhaps even catastrophically: through the trace-element. On this we have no more than scattered evidence, and the following discussion must be regarded as highly speculative.

The cyclic plagues of lemmings as well as of voles, mice, rats, Arctic hares, and grey squirrels, and with them the inevitable increases in the numbers of their predators, have attracted a good deal of attention but there has been virtually no analysis of them, of the numbers involved or of their causes. In the first stage there is a vast increase of population, building up over a period of years. Then come the mass migrations, and, in the lemmings,

the columns of teeming millions fanning out on a broad front, marching on and on until they finally commit suicide in the sea in their hundreds of thousands. Apparently the gemsbuck, before man thinned its ranks, was given to a similar behaviour, also ending in a mass suicide in the waters of the South Atlantic, and every now and then one comes across a similar story for another species, usually a small mammal. Usually the story is of a column of animals having been seen, say of water shrews, which are normally fairly solitary. There can be little doubt that all these, well-known or fragmentary, stories belong to a related plexus of behaviour.

So far the only explanation advanced is based upon investigations carried out in recent years on the lemmings. If the results obtained are correct then we must believe that these phenomenal increases in population, the mass migrations and fantastic suicides are the result of eating a particular lichen. The story does not end there, however. Apparently the lichen contains a vitamin which affects the anterior lobe of the pituitary, and through it the reproductive organs, giving a tremendous fertility. This becomes cumulative over the years. Moreover, it seems to impart a fearlessness, which accounts for the fact that the timid lemming marches in column with no thought of individual safety.

The sequel seems to be even more extraordinary. The predators, the owls, hawks, foxes and so on, after gorging themselves on "vitamin-drunk" lemmings become almost as fearless as they.

The lemming story does not differ fundamentally from that of the oyster, whose spat cannot survive in water containing copper in less than one part in 700 million. It is believed, though not proven, that certain species of diatom provide this in the oyster beds, and that oyster beds without these diatoms are likely to be barren.

It is not known why the common frog emerges from hibernation simultaneously over a wide area for the breeding assemblies. Weather conditions do not appear to offer an explanation: the time may vary from the end of January to the beginning of March. Nor is it known why, on occasions, the frogs may assemble at the pond, yet not begin to breed for several days. It is suspected that the smell from the algae necessary for feeding the tadpoles is the trigger which brings the frogs into breeding condition.

It is known that lions dig up a certain bulb and eat it; that the intensely carnivorous polar bear sometimes fills its paunch with vegetation; that most carnivores take some vegetable matter at some time or another. But nobody knows why, and nobody seems to have tried intensively to find out.

Major Anthony Buxton has studied the roe rings, has collected all the plants in these rings and finds that the one species common to roe rings is ergot. He suspects that eating ergot is a stimulant to breeding. His suggestion has not met a ready acceptance.

Yet, against all these things we have a counter-mystery. The cycle of reproduction has been traced from the secretion of a hormone by the anterior lobe of the pituitary. It has been completely studied except for one thing: What stimulates the pituitary to secrete the hormone? Is it the result of an internal rhythm, inexplicable and beyond our comprehension, or is it the result of a trigger action from something in the diet, a lichen, ergot, a bulb, an alga, a paunchful of greenstuff or some such thing?

There may be nothing in all these things but coincidence. Or it may be that vegetable protein only is necessary. It may be that a small group of plants of widely differing taxonomic relations is involved; or it may be, in perhaps the minority of cases, that a single species is involved. These things we do not know, for apart from Major Buxton, nobody seems to have investigated a single case in sufficient detail to give an answer.

Most birds have a uro-pygial gland at the base of the tail (the so-called parson's nose). Its function has long been a mystery, and probably is still, but it appears to depend on a trace-element. Fabricius found that nestling tufted duck fed on *Daphnia* were healthy and could swim. When the diet was changed to crushed fish, hard-boiled eggs and bread-and-milk, they became unhealthy and their feathers waterlogged when placed on water. They were sufficiently unhealthy that three out of five died in a few days. When the survivors were fed on water snails and swan mussels, they regained their health but the plumage was still not waterproof, until they were fed on grasshoppers.

A similar thing was found for other species of ducks, and there is the clear indication that the Arthropod (crustacean or Insect) protein is needed to keep the preen-gland of ducks functioning. But what is the ultimate source of the essential materials? Presumably it is vegetable in origin and presumably common to a number of species of plants. It is not impossible, however, that a given species of duck could depend for the essential material for its preen-oil, through its insect food, on a single species of plant and if that were removed suddenly ("a *Zostera*-incident") the duck could die out.

The paper was discussed as follows:—

Dr. Butcher said that he was very interested in Dr. Burton's remarks about the possibility that the smell from algae provided the "trigger" which brings frogs into breeding condition. Algae have characteristic odours which are sufficiently marked for the human sense of smell to be able to distinguish between those of certain species. He was impressed by the ability of animals sometimes to distinguish between plants—for example the only grass which his dog would eat is *Agropyron repens*.

Dr. Heslop-Harrison suggested that in connection with Dr. Burton's comments on the olfactory sensitivity of frogs and Dr. Butcher's on the odour of algae, it is interesting to recall some recent American work on the river specificity of fish. As is well known, Salmon will return to the river in which they were born to spawn, even after long intervals at sea, and when there are a large number of possible rivers to choose from. It has now been shown experimentally that fish can detect and remember subtle combinations of river "odours" in the water, and that these odours are organic in nature. They are actually volatile organic products, almost certainly arising from the algae growing in the higher reaches of the river, each river having its own special combination.

Prof. Tutin stated that when *Zostera marina* was abundant in parts of our coast it supported characteristic animals. When it diminished in 1930 certain molluscs and a hydroid associated with it disappeared from the neighbourhood of Plymouth.

Dr. Burton, in reply, said that this was an example showing that the dying out of a plant species entailed reduction and hardship for animal species rather than their extinction. The hydroid *Lucinaria* which was associated with *Zostera marina* was now found on other food plants.

Prof. Osborn said that when he was at Adelaide he was responsible with Wood-Jones for the introduction of the koala from French Island into part of Kangaroo Island. It was now thoroughly established there feeding on the shoots of *Eucalyptus*. There might perhaps be some species in common between the two islands, but the general assemblage of Eucalypts was somewhat different. Dr. Burton's remarks reminded him of another Australian example of the relationship between an animal and plants. He was with Bateson in the Adelaide Hills in 1913 when Bateson caught a wanderer butterfly. The larvae of this insect are believed to feed only on asclepiads and these were then unknown in the locality. Subsequently one introduced species was found.

Dr. Gordon Haskell said he would like to add another example to those mentioned by Dr. Burton. Maize is indigenous to some parts of the United States. Sweet corn is a sugary form of maize sometimes grown in England, and this is sometimes violently attacked by frit fly (*Oscinella frit*). Out of 80 different strains examined he had not found one completely resistant to the insect, yet the English strains of the fly, which normally attack oats, have never before had the opportunity of being selected for their ability to attack maize. This is especially interesting as frit flies in America, which are regarded as morphologically similar to the English strains, do not attack maize there. Some experiments were made by growing sweet corn and oats together in the expectation that the frit fly would attack oats in preference to the maize. But the maize still suffered, and was perhaps even preferred. Thus it appears that we cannot predict what changes in our cultivated plants may do to the food habits of our fauna. This may, in turn, have repercussions on the natural flora.

BRITISH VEGETATION IN THE FULL-GLACIAL AND THE LATE-GLACIAL PERIODS

H. Godwin,

The penetrating and extensive studies of the Late-glacial period made throughout Western Europe in the last two decades have been richly supplemented by those of Jessen (1949) and Mitchell (1951) in Ireland, and by others somewhat less frequent in Great Britain. In consequence of these investigations, there can remain no doubt that the Allerød climatic oscillation at the close of the last Glacial period has been adequately identified over a large part of the British Isles and this carries with it the recognition of the immediately preceding and succeeding cold periods, which as Zones I and III of the pollen analysis zonation make up, with Zone II of the Allerød period itself, the 'Late-glacial' in its present restricted usage. Exactitude is given to this terminology by the fact that the Allerød has been clearly identified as the Gotiglacial stage of ice retreat from Southern Scandinavia, and Zone III (equivalent to the Upper Dryas clay) as the stage of formation of the Norwegian Raa, the middle Swedish moraines and the Finnish Salpausselkä. In Ireland we have the Athdown Mountain Glaciation in Zone III separated by the mild Allerød stage from the latest stage of the Midland General Glaciation of that country.

This degree of assurance makes it desirable, and helps to make feasible, the separate recognition of deposits of the last glacial period itself as distinct from those of the Late-glacial above defined on the one side, and those of the last Interglacial on the other. From Denmark we have excellent evidence of the character of the last, the Eemian, interglacial of which it suffices to say that it clearly represents a period of some thousands of years' duration, during which there was a full climatic cycle from arctic tundra, through coniferous and birch forest stages to the deciduous forest phase of a climatic maximum, and back by coniferous forest again to arctic tundra. It was a long period characterised at its height by warmth-requiring species of plants and animals, and impossible, in well-developed form, of confusion with deposits of the glacial period which followed it. In the British Isles it has been recognised in a few places, and at one (Histon Road, Cambridge) a moderately long segment of the interglacial has been subjected to pollen-analysis (Hollingworth, Allison & Godwin, 1950).

Between the deposits of this interglacial and those of the Late-glacial period *sensu stricto* must come in point of time those of

the last glacial period itself. One need hardly stress the significance of the recognition of such deposits, which we may term "Full-glacial", for an understanding of the nature of climatic and biotic conditions in the last glacial period, and for assessment of the possibilities of survival or extinction of biota through that time. There are two series of British deposits which have, in my view, very strong claim to be regarded as 'Full-glacial', the so-called 'Arctic Bed'[1] described from many sites in the Lea Valley, north of London, at the 'Ponders End' stage of the evolution of the valley (Warren, 1912, 1916, 1923; Reid, 1949), and the 'Arctic Bed' of Barnwell Station, Cambridge (not to be confused with the older Barnwell Abbey beds) (Chandler, 1921). The evidence upon which this assignment rests is threefold: geological, faunistic and floristic.

Zeuner (1945) has already made a tentative correlation of the Lea Valley Arctic Beds with stages of the last glaciation, a correlation essentially based upon the levels and gradients of the Lea Valley and those of the later stages of the Thames valley. He accepts the view that the last Glacial period is represented by three cold phases and two interstadials, as indicated for instance by the Fläming or Warthe, the Brandenburg and the Pomeranian moraines of the Scandinavian glacial area. In the first cold period (Würm I or LG1) he places the erosion of the Hedge Lane Channel, and this was filled in during the following interstadial in consequence of the restoration of sea-level which built the 'Lower Flood-plain Terrace'. In the second cold period (Würm II or LG2) came the cutting of the Ponders End channel to a gradient distinctly below that of the Hedge Lane channel, and this was filled in during the second interstadial (LG2/LG3). Finally, during the third cold period (Würm III or LG3) he suggests there was the cutting by the Thames of the Tilbury channel which has been filled in during the Post-glacial period. Without necessarily accepting this detailed correlation, we can take it as showing that the geological evidence points clearly to a Full-Glacial age for the Arctic Beds of the Lea Valley. When Zeuner made this correlation the Nazeing channel stage of the Lea Valley had not been described (Allison, Godwin & Warren, 1952), but there is no doubt that it agrees in level and in age with the Tilbury channel. Pollen-analyses through its infilling of peat and calcareous muds show uninterrupted progress of deposition from Zone III at the close of the Late-glacial period through to the deciduous forest stage of the Post-glacial. The base of the channel contains some slightly older material, partly fluviatile and partly lacustrine, which may be Late-glacial or may represent the last cold period of the Full-glacial. The dating of the channel filling not only establishes the age of cutting of the Nazeing chan-

[1]The 'Arctic Bed' of the Lea Valley has hitherto been written of as a 'Late-Glacial' deposit, but this does not conform with the more exact modern usage of that term, and ought, I suggest, to be abandoned.

nel itself as within the last glaciation, but places the deeper-lying 'Arctic Beds' with certainty into the Full-glacial. Pollen-analysis of the 'Arctic Beds' themselves has not so far proved practicable, but an attempt at radio-carbon assay kindly made by Libby (Godwin, 1951) has given a result of >20,000 years, a value amply sufficient to place it earlier than the Late-glacial (*s.s.*), the date of which (the Allerød period) has been independently determined by the same method for various sites in the British Isles and the continental mainland.

Now that Iversen in Denmark, and Jessen and Mitchell in Ireland have assessed the animal life of the Late-glacial period, it has become clear that the 'Park-tundra' of these areas supported a fauna characteristically rich in large herbivorous mammals such as horse, elk, reindeer, bison and giant Irish deer. Although the mammoth (*Elephas primigenius*) has once been found in the Late-glacial, this animal and the woolly rhinoceros (*Rhinoceros antiquitatis*) are more characteristic of the Full-glacial and certainly lived in Western Europe during the last glaciation. These remains are quite typical and abundant in the Lea Valley Arctic Bed, where to be sure, they are accompanied by frequent bones of horse, some reindeer and probably by bison. The smaller mammals afford a less certain basis for distinguishing between the Arctic Bed and the Late-glacial of the Lea Valley, but the mollusca, abundant in deposits of both periods, *are* of value for this purpose. Kennard (Warren, 1912) distinguished the rich Lea Valley Arctic Bed assemblage from those of all other Pleistocene deposits and suggested that they indicated a July isotherm of 8° to 10°C for the period of their origin. He distinguished two groups of mollusca, the one containing truly boreal species, such as *Sphyradium columella, Vertigo parcedentata, Planorbis arcticus* and *Jaminia muscorum* var. *lundstroemi,* and the other consisting of dwarfed individuals of species having a wider distribution. The Late-glacial molluscan assemblage of the Nazeing Channel lacks representatives of the former (boreal) group but represents a "modified survival of the stunted fauna of the Arctic Plant Bed" and Mr. Warren (Allison, Godwin & Warren, 1952) points out also certain further notable modifications.

We shall later see that the floristic evidence bears out the strong probability that the 'Arctic Bed' deposits belong to a period distinctly different from, severer than, and older than those of the Late-glacial *s.s.,* and may thus most reasonably be referred to the 'Full-glacial'. It has so long been customary to consider the Arctic Bed of the Barnwell Station pit at Cambridge as of the same age as the Ponders End Arctic Bed that we need not reiterate the arguments on which this is based: we fully accept the view that it must be regarded as Full-glacial also.

The correlation table given in fig. 1 expresses some of the main features of presumed correlation between the British or West European deposits with which we are concerned. It will be noted

S. Scandinavia	Common ground				Ireland	Great Britain [STAGES AND SITES]
	PERIOD	AGE	POLLEN ZONES	PERIOD		
	Post glacial	8,000	VII	'ATLANTIC'	very numerous sites	very numerous sites
			VI	'BOREAL'		
			V			
FINI GLACIAL			IV	'PRE-BOREAL'		
MIDDLE SWEDISH MORAINES	Late glacial	10,000	III	YOUNGER DRYAS		VALLEY GLACIATIONS PERTH READVANCE
GOTI GLACIAL			II	ALLERØD	Ballybetagh Kilaghan etc.	Whitrig Hockham Windermere Star Carr Neasham Garscadden Hawks Tor Nazeing etc
BALTIC END-MORAINE		12,000	I	OLDER DRYAS	?	SCOTTISH' READVANCE
DANI GLACIAL		14,000		? BØLLING oscillation		
POMERANIAN END MORAINE ?	Full glacial ↓	?	WEICHSEL GLACIATION			NEW PONDER'S END Lea Valley 'Arctic Bed' Barnwell Station DRIFT
BRANDENBURG END MORAINE					MIDLAND GENERAL GLACIATION	

Fig. 1.

that the Late-glacial can be approximately dated as between 10,000 and 15,000 years of age, vastly shorter than the Full-glacial which preceded it. The correlation with continental stages, especially for the Full-glacial, is meant only as tentative and general.

We have not elaborated the correlation or sub-division of the Post-glacial period, the stage of climatically improved conditions including the Post-glacial climatic optimum and extending to the present day. Throughout the lowlands of the British Isles it has been a period of woodland dominance, of birch and locally of pine in the earliest stage (Zone IV) but afterwards of pine and of the mixed-oak-forest components with *Corylus* and *Alnus,* later still with the addition of *Fagus* and *Carpinus* in southern England.

The task of correlating the Full-glacial and Late-glacial stages with the direct field evidence for the position of the British ice of the last glaciation is as yet barely begun. It seems likely that Zone III, the cold spell closing the Late-glacial was represented

by valley glaciations of small magnitude in the Scottish highlands, the Lake District and Wales. Zone I has been taken to correspond with the Scottish Re-advance (represented by the Boulder clays extending south from the Southern Scottish Uplands over the western Lake District and parts of the Isle of Man). Support is given to this view by the certain recognition of the Allerød deposits within the area of the Scottish Re-advance at Whitrig Bog in Berwickshire, and at Garscadden Mains near Glasgow (Mitchell, 1952). The equivalent of the Scottish Re-advance in Ireland is not yet certain, but may be the Athdown Mountain Glaciation in Wicklow. Far outside the limits of the Scottish Re-advance lies the boundary of the 'New Drift', extending from Filey in N.E. Yorkshire across the Vale of York, and diagonally across England to South Wales, and crossing Ireland from just north of Wexford to the estuary of the Shannon. We must suppose that the Full-glacial deposits formed in the period of the New Drift, in the milder stage between that and the Scottish Re-advance, and possibly within still undetected stakes of advance to, or oscillation within the New Drift.

It will be recognised that, even were the Lea Valley and Barnwell Arctic beds formed at the period of greatest extension of the New Drift, the glacial margin of that time would, nevertheless, have been at least 100 miles (160 km.) to the northwest, and if they formed during a recession (as seems more likely) then the distance may have been considerably greater. In either event, they appear to be sufficiently related to the maximum extension of the last ice sheet for their floras to be taken as characteristic of British plant life during the severest or almost the severest part of the last glacial period. Members of the fossil floras of the period may be taken in general to be either perglacial survivors or species which, if incapable of persistence in the most exacting stages of the glaciation, nevertheless were present by immediate colonisation after amelioration.

There are two ways of investigating the flora of the Late-glacial and Full-glacial deposits; for the Late-glacial beds, both pollen-analysis and identification of macroscopic plant remains have been practised; for the Full-glacial deposits, the latter method only. Whilst the strength of pollen-analysis lies in the general picture which it is able to convey of the vegetational picture and so of climatic and biotic conditions, that of the identification of macroscopic remains lies in the much greater security of specific recognition and the greater likelihood that the plants actually grew close to where their remains have been found. It goes without saying that there is a very great advantage in combining the two largely complementary methods.

Pollen analyses from deposits of Late-glacial age have shewn that, taken as a whole, it had vegetation of the character of 'Park-tundra'. The high ratio of non-arboreal to arboreal pollen be-

speaks an open landscape with scattered clumps of birch trees, although closed birch woodlands (with pine in Holstein) characterised the milder Allerød period itself. Sedges and grasses contributed very largely to the herbaceous pollen, but along with these many other types occur with high constancy, and often with high frequency, for example *Armeria, Artemisia, Campanula, Centaurea, Epilobium, Filipendula Ulmaria, Galium, Helianthemum, Plantago media, Polemonium coeruleum, Ranunculus, Rumex, Sanguisorba officinalis, Succisa pratensis, Thalictrum, Valeriana officinalis, Selaginella selaginoides, Botrychium, Lycopodium,* and *Ophioglossum.* Pollen of *Caryophyllaceae* and *Chenopodiaceae,* of *Labiatae, Umbelliferae* and several types of *Compositae* occurs abundantly and confirms the general picture of a rich herbaceous vegetation. Less abundant but equally informative pollen records are those for *Centaurea cyanus, Linum, Scleranthus* and *Pastinaca sativa. Empetrum nigrum* pollen is often abundant, especially in the more Atlantic regions as Jessen has pointed out for N.W. Ireland during Zone II. The abundant birch pollen comes partly from *Betula pubescens,* partly from *B. nana,* and the willow pollen partly from *Salix herbacea* (which in Ireland strongly characterises Zones I and III) and partly from other species such as *S. phylicifolia.*

Jessen and Mitchell have identified much macroscopic plant material of Late-glacial age from Ireland, Mitchell and Miss A. P. Conolly have made several records from two Scottish sites, and several workers have contributed to the records for various sites in different parts of England. Possibly the most prolific of these have been Hawks Tor in Cornwall and Nazeing in the Lea Valley, both sites of special interest lying far south and distant from the edges of the dying ice sheet.

From these sources it has been possible to put together a floristic list for the Late-glacial of the British Isles to set alongside the very full and careful records for the early Full-glacial worked out for Barnwell and the Lea Valley Arctic Bed. The following lists are based for convenience upon the phytogeographic categories devised by Matthews (1937), but they include also species no longer native here. The species which Matthews placed in his category of wide European and extra-European range have not been dealt with.

The question mark in the lists indicates a merely tentative identification and the bracketed records for Scotland are from old sites taken to belong to the Late-glacial upon somewhat doubtful evidence.

It will be appreciated that with so much active research in progress these lists are out of date almost from the moment that they are made, and during even the last month [March 1952] Mr. Frank Mitchell has made many notable additions to the Irish list.

TABLE 1.

BRITISH FULL-GLACIAL and LATE-GLACIAL PLANTS.

A. Arctic-Alpine "Historical Northern" (Matthews).

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Arabis petraea			?			?
Arctostaphylos uva-ursi ...		+	+	+		
Betula nana	+	+	+	+	+	+
Carex incurva (*maritima*) ...		+				
C. atrofusca (*ustulata*) ...		+				
C. capillaris	+					
Draba incana	+	+	+	+	+	+
Dryas octopetala	+		+	+	(+)	+
Empetrum nigrum			+	+	+	+
Polygonum viviparum	+	+				
Salix lapponum	+					
S. reticulata	+		+	+	+	+
Thalictrum alpinum	+	+	+	+	+	+

B. Arctic-Alpine "Historical Tertiary".

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Arenaria ciliata agg.			+	+		+
Carex atrata		+				
C. lagopina	+					
Cerastium alpinum			?	?		
Eriophorum angustifolium ...	+	+	?			
Loiseleuria procumbens					(+)	+
Oxyria digyna		+	+	+	(+)	+
Potentilla Crantzii		+	+	+		
Salix arbuscula	+					
Saxifraga oppositifolia	+					
Vaccinium uliginosum	+					

C. Species no longer Native.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
1. Montane, arctic and alpine.						
Arenaria biflora	+					
(*Betula nana* in Ireland) ...	+	+	+	+	+	+
Papaver alpinum	+					
Potentilla nivalis		+				
P. nivea		+				
Pedicularis hirsuta		+				
Ranunculus aconitifolius ...	+	?				
R. hyperboreus		+				
R. nemorosus		+				
Salix polaris	+		+		(+)	

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
2. Totally extinct.						
Silene coelata Reid	+	+				
Linum praecursor Reid ...	+	+				
3. Continental.						
Gentiana cruciata	+					

D. Alpine.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Arenaria sedoides	+					
Saxifraga hypnoides			+			+

E. Arctic Subarctic.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Cornus suecica		?				
Primula scotica	+					

F. Northern Montane.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Arenaria gothica		+				
Polemonium coeruleum ...			+	+		
Potentilla fruticosa	+		+	+		
Primula farinosa		?				
Rubus saxatilis			+	+		
Salix phylicifolia			+	+		
Subularia aquatica			+	+		

G. Continental Northern.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Andromeda polifolia			+	+	(+)	
Betula pubescens			+	+	+	+
Carex disticha			+	+		
C. pulicaris		+	+	+		
Cicuta virosa			+	+		
Cirsium heterophyllum ...		+	?	?		
Comarum palustre		+	+	+	+	+
Eleocharis multicaulis			+			+
Littorella lacustris		?	+	+		+
Viscaria alpina	+					
Menyanthes trifoliata	+	+	+	+	+	+
Potamogeton filiformis	+	+	+	+	+	+
P. obtusifolius	+	+	+	+		+
P. praelongus		+	+	+	?	+
Potentilla procumbens	?					
Salix aurita			?			?
Sparganium angustifolium ...			+	+		
Vicia sylvatica		+				
Viola palustris	+		+	+	+	+

H. Continental.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Holosteum umbellatum ...			+	+		
Potentilla argentea	+					
Ranunculus Lingua	+		+	+		+

I. Continental Southern.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Oenanthe Lachenalii			?		(+)	

J. Oceanic Northern.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Cochlearia danica	+					
C. officinalis			+			+
Naias flexilis			+	+		
Silene maritima		+				

K. Oceanic West European.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Carum segetum			+	+		
E. tetralix			+	+		
Myriophyllum alterniflorum ...		?	+	+	+	+

L. Oceanic Southern.

	Barnwell.	Lea V.	Late Gl.	Late Glacial. Eng.	Scot.	Ir.
Damasonium Alisma		+				

M. Mediterranean.

Not represented.

A, B. *Arctic-alpine.*

Taking the Full-glacial and Late-glacial records together, they include one-third of the present British Arctic-alpine element, 26 out of a total of 76, the Full-glacial contributing a somewhat larger proportion than the Late-glacial to this number. Some species occur both in the Full- and in the Late-glacial lists, but whilst chance must be largely responsible for this, it is noteworthy that the two Arctic willows, *Salix arbuscula* and *S. lapponum,* have not yet been found in Late-glacial beds. It seems highly probable that plants in this category survived the last glaciation in Britain. Their Late-glacial distribution areas were in many instances very much wider than their present ranges, a fact illustrated by the distribution maps for *Betula nana, Thalictrum alpinum,* and *Salix herbacea.* This restriction of range must be considered due to the conditions of the Post-glacial period, whether caused directly by climatic change or indirectly through the operation of other causes.

C. *Extinct plants.*

Two plants now no longer known living have been recorded from the Full-glacial deposits. One, *Silene coelata* Reid, rests upon evidence which makes it certain that it was a distinct species, the other, *Linum praecursor* Reid, is open to some doubt since it seems closely similar to *L. anglicum.* However, Miss J. Allison has found specimens precisely matching *L. praecursor* in East Anglian interglacial material. Among species still living but not found in Britain, *Gentiana cruciata* has a continental distribution, but the rest are montane, arctic and alpine. If we except the dubious record of *Salix polaris* from the Scottish Lowlands, all the extinct species come from the Full-glacial deposits, but one naturally cannot say whether the extinction was attributable to Post-glacial or to earlier conditions.

That extinction of Arctic-alpine plants *has* occurred in the Post-glacial period is shown by the case of *Betula nana* which has now been found in Ireland in the Late-glacial, although the plant is no longer living there. Doubtless many more remain to be added to this list. It is interesting to note that *Papaver alpinum* L., *Arenaria biflora* L., *Potentilla nivalis* Lapeyr., are high alpine plants, *Gentiana cruciata* is also alpine and their presence in the Full-glacial is in line with a relict explanation for the present disjunct northern distribution of alpine species. *Potentilla nivea* agg. is arctic-alpine, and *Ranunculus hyperboreus* a high arctic species. *Pedicularis hirsuta* is an 'Amphi-Atlantic' arctic plant of limited occurrence in northern Scandinavia. It is not quite clear to what groups the identifications of *Ranunculus aconitifolius* and *R. nemorosus* refer.

D. *Alpine.*

One of the nine species in Matthews' Alpine element is recorded in the Full-glacial and one in the Late-glacial.

E. *Arctic-Subarctic.*

Of the 30 species placed by Matthews in the Arctic-Subarctic element, two (one doubtful) have been recorded from the Full-glacial, none from the Late-glacial.

F. *Northern montane.*

Of 25 species in the Northern Montane element, two (and one doubtful) have been recorded from the Full-glacial, and five from the Late-glacial. Among them there are further instances of restriction of range since the Late-glacial period. Particularly notable is the case of *Polemonium coeruleum* which has a very restricted and scattered range to-day: its complex and characteristic pollen grains have now been found in a number of Late-glacial deposits in various parts of England from Cornwall, Surrey, and Shropshire to Yorkshire, lying far outside its present area. *Subularia aquatica* with a pronouncedly northern range in Britain has been recorded from the Late-glacial in Cornwall, and

Potentilla fruticosa with a notably restricted and disjunct distribution to-day occurred in both the Full- and Late-glacial outside its present range.

G. *Continental Northern.*

Matthews has placed 91 British species in his Continental Northern Group; ten (plus two tentative recognitions) have been recorded for the Full-glacial, and fifteen (again plus two tentative recognitions) from the Late-glacial. As might be expected, a number of these records lie to the south of the present range of the species concerned.

H. *Continental.*

Of the 82 species placed in Matthews' Continental element one occurred in the Full-glacial, one in the Late-glacial, and *Ranunculus lingua* was found in both. The most remarkable of these records is that made by Mr. P. A. Tallantire of *Holosteum umbellatum* from the Late-glacial of East Anglia.

I to M. *Other geographic groups.*

The Continental Southern element, in which Matthews has placed 127 British species, has only a single dubious record from the Late-glacial, but the Oceanic Northern, containing 19 species, has two records from the Full-glacial, and two from the Late-glacial. *Naias flexilis,* however, is certainly more characteristic of the early Post-glacial than of the Late-glacial, and is often very abundant in Irish lake deposits of the younger period. The present restriction of range of this species must then certainly be regarded as a Post-glacial phenomenon. The Oceanic West European element, which contains 76 species, has one tentative record only for the Full-glacial, whilst in the Late-glacial there are three. *Myriophyllum alterniflorum* has been doubtfully recorded from the Full-glacial, but its pollen has been seen in Late-glacial deposits in England, Scotland and Ireland, and has indeed long been recognised as characterising deposits older than the Boreal period. The one record of *Damasonium Alisma* from the Full-glacial in the Lea Valley alone represents the 74 present species of the Oceanic Southern group: although the identification is beyond question and the fragile nature of the carpels seems to preclude the possibility that it has been secondarily incorporated in the 'Arctic Bed' at Hedge Lane its presence then appears anomalous. Unfortunately, the stratigraphic situation at this site was complex and never properly resolved. The Mediterranean group, in which Matthews places 38 species, has no representatives in the Full- and Late-glacial records. The percentage Late- and Full-glacial representation of the present British flora in the different geographical groups is given in Table 2. The Arctic-alpine is most strongly represented; but the Northern Montane, Alpine, Continental Northern, and Oceanic Northern are almost as abundant. As we have pointed out, in the extinct

species and Arctic-alpines the Full-glacial has the heavier representation, but in the Continental Northern and Northern Montane the preponderance is in the Late-glacial records.

TABLE 2.

BRITISH FULL GLACIAL AND LATE GLACIAL PLANTS.

Analysis of Species Identified in Matthews's Groups.

Group size.		Full Glacial. Barnwell.	Lea V.	L.G.	Total.	% of present Br. flora in the category.
38	Mediterranean	0	0	0	0	0
127	Continental Southern	0	0	?	?	?1
74	Oceanic Southern	0	1	0	1	1
76	Oceanic W.-European	0	?	3	3	5
82	Continental	2	0	2	3	4
19	Oceanic Northern	1	1	2	4	21
91	Continental Northern	4?	9?	15??	19	21
25	Northern Montane	1	1?	5	7	28
76	Arctic Alpine	14	11	13?	26	34
9	Alpine	1	0	1	2	22
30	Arctic Subarctic	1	?	0	2	7
—	Montane-Alpine non-native	5	5?	?	10	—
—	Extinct	2	2	0	2	—

(? signifies a dubious identification)

A further difference which emerges from comparison of the full records is that, apart from *Juniperus* (and pollen possibly derived or wind-carried from a distance), trees are unrepresented in the Full-glacial lists, whereas the Late-glacial records include *Betula pubescens* (the most abundant tree), *B. pendula,* their hybrids with *Betula nana, Sorbus* (most probably *S. aucuparia*), and *Populus tremula.* It is as yet uncertain whether *Pinus* was present, for macroscopic records are lacking and pollen, although often quite abundant, is insecure as an index of immediate presence.

It would appear from these comparisons that although the Full- and the Late-glacial records shew considerable similarity in floristic composition there is a definite indication of greater climatic severity in the Full-glacial, as already the molluscan and glaciological evidence have shewn.

Certain other features emerge from a consideration of the records from a slightly different angle: when grouped ecologically rather than phytogeographically it becomes apparent that two categories bulk particularly large in the lists both of the Full-glacial and of the Late-glacial. The first of these is roughly defined as "Aquatic or Marsh plants," their prevalence no doubt in part due to the preference given to such species by the conditions of preservation, and partly to the wide geographical and

climatic range of plants in this category. Their abundance is reflected both in pollen and in seed records.

The second group is that of ruderals or weeds, and here the very long list must indicate the prevalence of open conditions, bare soil surfaces and freedom from competition. It will be noted that Polunin has strongly emphasised that plants of his category of 'Arctic' species demand these conditions also. These identifications make it evident that many weed species hitherto thought to be introductions to Britain by Neolithic and later agriculturalists are of much older standing. We may note especially *Linaria vulgaris, Galeopsis Tetrahit, Polygonum aviculare, Sonchus arvensis, Taraxacum officinale, Stellaria media, Cerastium vulgatum, Ranunculus acris,* and *R. repens* and the abundant pollen of *Rumex, Artemisia,* and other *Compositae.* Mr. Tallantire has found a single grain of *Centaurea Cyanus* (a species already known from the Danish Late-glacial) and we may recall the pollen identifications also of *Plantago media* and *Pastinaca sativa.* It may well be said that there is nothing here which disproves the suggestion that they may have been subsequently extinguished and later reintroduced, but in several instances repeated discoveries at all stages of the Post-glacial render such an hypothesis unnecessary.

These positively dated records bear out in striking manner the opinion expressed by Salisbury as long ago as 1932 when he wrote of 'the considerable area of morainic deposits that must have fringed the European ice front throughout the pleistocene glaciations', that "It is not improbable that this was the primary home of species which to-day are mainly, if not exclusively, associated with the artificial conditions of cultivated and disturbed soil".

It is apparent that these species, suppressed and restricted by the closed forests which covered the lowlands, and the peat mires which covered much of the uplands, survived the greater part of the Post-glacial period on cliffs, beaches, river-banks and screes until the destruction of the native forest by prehistoric man gave them opportunity to expand once more. That such species can have a place in the British Flora irrespective of human introduction is clearly shewn by the numerous ruderals and weeds represented in the river channel deposits of the Clacton Interglacial, for although man was present then his numbers and influence were doubtless small.

As a final comment upon the lists of identified species from Full-glacial and Late-glacial deposits it may be noted that species characteristic of the undergrowth of deciduous woodlands are totally or almost totally absent, and that the presence of such species as *Calluna vulgaris, Erica Tetralix, Petroselinum segetum* and *Empetrum nigrum,* the latter abundant, reinforces Jessen's view that the Late-glacial climate of the British Isles must have had a definitely Atlantic character then as now. These species have not been found in the Full-glacial.

To conclude, the evidence shews the Full-glacial landscape in Britain to have been a tree-less tundra and that of the late-glacial to have been treeless or lightly wooded 'Park-Tundra'. In both, there was a herbaceous flora rich in species especially of the categories of ruderals and weeds, aquatic and marsh plants: the chief phytogeographical caegories present were Arctic-alpine, Northern Montane, Continental- and Oceanic- Northern, and Alpine, but there were present also large numbers of plants of wide general distribution. The flora in Late-glacial time had some oceanic tendency. At this time open habitats and fresh soils abounded, and dispersal was easy for species without exacting warmth requirements; since the North Sea basin was dry during Full- and Late-glacial time, spread from the Continent was also easy. The evidence shews that many plants were widespread at this time which now have a restricted and disjunct areal distribution.

In the Post-glacial period the spread of forest, coupled with progressive leaching of soils and the spread of mires in forest-free areas, has greatly restricted the range of all species requiring open habitats. Where dispersal *had* been easy and rapid for them, it *now* became slow or ceased. In short, we cannot doubt that these *Post-glacial* events have been responsible for some, and perhaps many, of the so-called 'relict' distribution ranges hitherto explained as due to survival "in situ" through the last glaciation. Although the Full-glacial records go far towards shewing us the nature of perglacial survivors in this country, the significance of this is lessened by the realisation that their present ranges have been determined not so much by the localities of such survival, but by later events.

The realisation that phases of rapid and general dispersal may alternate with phases of fixity, adds much to our resources in interpreting contemporary distribution phenomena, especially when it is understood that phases favourable for the spread of one category of plants may be unfavourable for others.

The analysis we have attempted has been restricted to data from the Full- and Late-glacial periods, but similar information is available and becoming more abundant for Interglacial and Post-glacial deposits also. The extension of the records for identified plant remains from all these periods, dated precisely by pollen-analysis or other techniques, and visualised against a clear picture of the events of the Pleistocene period, will clearly afford the information we are entitled to regard as a factual basis for phytogeographic theory.

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This paper was discussed as follows:—

DR. DAHL asked if Dr. Godwin could state the total number of species now recorded from the Late-glacial. Dr. Godwin replied that it was of the order of 200.

MR. MILNE-REDHEAD enquired whether the pollen of *Diapensia lapponica*, a circumpolar plant recently discovered in Scotland, had been recorded from any of the deposits mentioned in the paper. Dr. Godwin, in reply, said that the pollen of this species was not easy to distinguish and he would prefer to identify it from macroscopic remains. It had not yet been recorded.

DR. BAKER said that all fossil remains of *Armeria maritima* examined in this country have been of the dimorphic subsp. *maritima*, which now extends from the north of the Iberian peninsula to southern Greenland. Therefore, it should not be classed as a member of an " Arctic-alpine " element, but rather as " Oceanic Northern." Dr. Godwin replied that there would have to be modifications of Matthews' lists but broad generalisations could be made on this basis. He agreed that there was no reason to suppose that any fossil material identified as *Armeria maritima* could not be included in the subspecies now found on our shores.

MRS. M. L. DAVIS asked if the pollen of *Stachys alpina* had been found. Dr. Godwin replied that it had not. He said that the pollen of Labiates was particularly difficult to identify and it must be remembered that it was usually not possible to identify species from pollen alone. Pollen was valuable for giving a general view of the vegetation: for the identification of species it was generally necessary to have macroscopic remains. The two methods had to be used together. Dr. Godwin said that in making identifications it was necessary to consider the whole background of the European flora and especially those species which now occur in Scandinavia.

Mr. Rose enquired whether the " Full-glacial " of Dr. Godwin's paper referred to the maximum glaciation in Britain when the ice sheet reached the vicinity of London. Dr. Godwin replied that this maximum glaciation was earlier than the one he had spoken of as the Full-glacial, and represented a much greater period back in time.

Canon Raven asked if the speaker could give any indication of how far the sites identified and examined could be regarded as representative and complete. Dr. Godwin said that for every site examined there must be thousands waiting to be done. For example, it was known that in Shropshire alone there were a very large number of end moraines full of material waiting to be worked. Seeds and fruits of dry-land plants were only preserved in steep-sided basins and the deposits could never be regarded as completely representative of the flora of the time they were laid down.

Prof. Webb asked if there were any fossil records of sycamore (*Acer Pseudoplatanus*) in Britain. This species was unique in the British flora, as a well-established alien, thoroughly at home here, whose native territory was not far away. Why it is not now native is rather puzzling, and it would be especially interesting to know if it ever had been. Dr. Godwin replied that fossil material of the sycamore had not been identified. He agreed that it was somewhat remarkable that it did not appear in the Post-glacial until introduced by man.

SOME LATE-GLACIAL PLANTS
(Exhibit)

D. Walker and R. G. West.

Dr. Godwin has already drawn attention to the differences between the 'full glacial' and 'late-glacial' floras recovered from peat and mud beds in Great Britain. It is with the strictly Late-glacial period and the Post-glacial period which followed it that this paper is primarily concerned.

Many Late-glacial deposits are now known in the British Isles but for the purposes of illustrating our main points we have chosen to consider a pollen diagram from the fen bordering Skelsmergh Tarn, a little north of Kendal in Westmorland at 400 ft. O.D. The work at this site has only recently been started and nothing more than a preliminary account is yet available.

The lowest metre of mud contains abundant pollen of herbaceous plants along with *Salix, Betula* and *Pinus* pollen. This stratum certainly covers the Late-glacial period, and the diagram clearly illustrates the threefold division into two tundra phases separated by a period of more or less closed birch woodland. Most of the *Betula* pollen belongs to the tree birches (fruits of *Betula pubescens* have also been recovered from these muds) but some certainly belongs to *B. nana,* a determination which we have been able to make following the publication by Terasmäe (1951) and the close examination of our own type material. It is significant that *Betula nana* pollen has never been recorded from the Skelsmergh deposits above the Late-glacial layers. We had tentatively referred some of the *Salix* pollen to *S. herbacea* (Straka, 1952) and this suggestion was rendered more plausible by the discovery of *Salix herbacea* leaves in the muds of the upper tundra zone.

Although grasses and sedges contribute much of the herbaceous pollen to the Late-glacial spectra, *Artemisia, Rumex, Thalictrum* and *Caryophyllaceae* contribute very substantial amounts; whilst *Helianthemum, Plantago media, Galium, Empetrum, Filipendula Ulmaria, Chenopodiaceae* and *Compositae* (additional to *Artemisia*) are consistently represented.

Whilst all trace of these herbs virtually disappears for the greater part of the Post-glacial period, some of them recover with the advent of human agriculturalists, probably during the Neolithic and subsequent periods (cf. Godwin & Tallantire, 1951). The grasses and sedges react most strongly to the clearance of the forests but *Artemisia* and other *Compositae, Rumex, Chenopodiaceae* and *Umbelliferae* also reappear in the pollen diagram at the same level and in considerable frequency. Some quite new

pollen types are also recorded and are very probably the result of human introduction, *Plantago lanceolata, P. major* and cereals being the most abundant.

These are all herbs which to-day are widely distributed over the British Isles wherever there are suitable fields or other clear spaces. Their occurrence in the Late-glacial is associated with the open habitats, often on unstable frost-moved soil, which seem to have been characteristic of the period in this region. Their distribution areas became dissected and restricted during the Post-glacial forest period, but there seems to have been no climatic barrier to their expansion when suitable habitats became available again (Godwin, **1949**).

A number of plants which we have come to recognise as typical of the Late-glacial period in northern England did not return to the lowlands after forest clearance and still have notably disjunct highland, coastal or northern distributions in Great Britain although apparently widely distributed during the Late-glacial. *Betula nana* and *Salix herbacea* are the most obvious examples of such plants which also include, in the Skelsmergh records, *Armeria maritima, Hippophaë rhamnoides, Selaginella cf. selaginoides* and *Lycopodium clavatum*. For some of these plants (e.g. *Armeria maritima*) it may be that some undetected feature of inland lowland ecology limits their extension, but with plants such as *Betula nana* it appears that it is a climatic barrier, perhaps the maximum summer temperature (Dahl, **1952**), which is active now but was not active during the Late-glacial period.

It remains for future research in both ecology and palaeoecology to shed further light on these problems. As Quaternary Research develops it becomes increasingly apparent where some of our major ecological problems lie.

We wish to thank Dr. H. Godwin, F.R.S., for his encouragement of this work and Mr. E. F. T. Elborne for taking the photomicrographs for the exhibit.

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PRESENT DAY AND LATE-GLACIAL DISTRIBUTION OF SOME ALPINE VASCULAR PLANTS IN SCANDINAVIA AND THEIR INTERPRETATION

(Exhibit)

EILIF DAHL (Oslo).

There are reasons to believe that many arctic-alpine plants are absent from the lowlands of Scandinavia not only because of competition but also because the climate is unsuitable to them. A number are of types which it is difficult to imagine would be exterminated by competition, and many are difficult to grow in gardens in absence of competition.

Observations on the behaviour of these plants in gardens as well as nature point in the direction that high summer temperatures are detrimental to them, for in gardens they tend to suffer during the particularly warm periods.

A confirmation of this hypothesis can be obtained by comparing the distribution of the alpines with the meteorological observations. The maximum summer temperature was selected for study since the plants seem to suffer during the warmest periods. From all meteorological stations in Norway, Sweden, Denmark, and Finland the average yearly maximum summer temperature has been calculated. This in itself will not help us much because the stations usually are situated in the valleys while the alpines grow in the surrounding mountains. The maximum summer temperatures on the summits can, however, be calculated because the temperature decreases with altitude in a fairly regular manner, 0.6° C. per 100 m. altitude. In this way has been calculated the maximum summer temperature in a very large number of the highest points in the terrain all over Scandinavia. From these it is possible to draw isotherms, the isotherm of 24° C. (see fig. 2) separates an area with summits with a maximum summer temperature of 24° or lower from an area where no such cool summits exist. And these isotherms are now compared with the distribution of the species.

As the first example (fig. 2), the distribution of *Poa flexuosa* Sm. is compared with the 24° C. isotherm. As will be seen the isotherm and the distribution limit coincides very closely. The absence of the species from the warm areas around Trondheim is especially instructive.

As the second example the distribution of *Sedum Rosea* (L.) Scop. is compared with the 25° C. isotherm. (fig. 3). On the south coast of Norway the species is confined to the immediate proximity of the sea with its cooling effect on the extreme summer temperature; the same applies to some localities in Bohuslan.

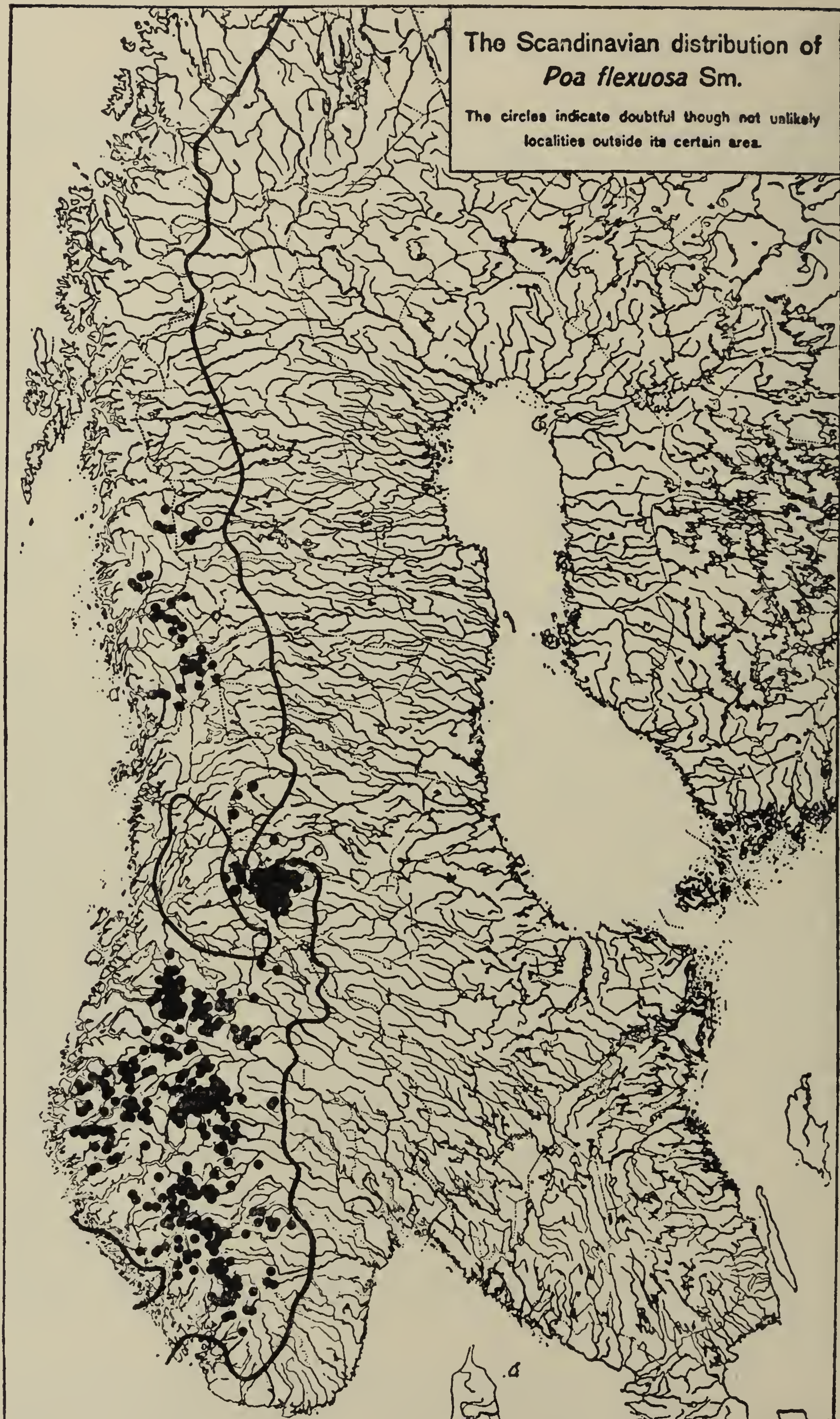

Fig. 2.

The Scandinavian distribution of *Poa flexuosa* Sm., according to Nannfeldt, with the 24° C. isotherm.

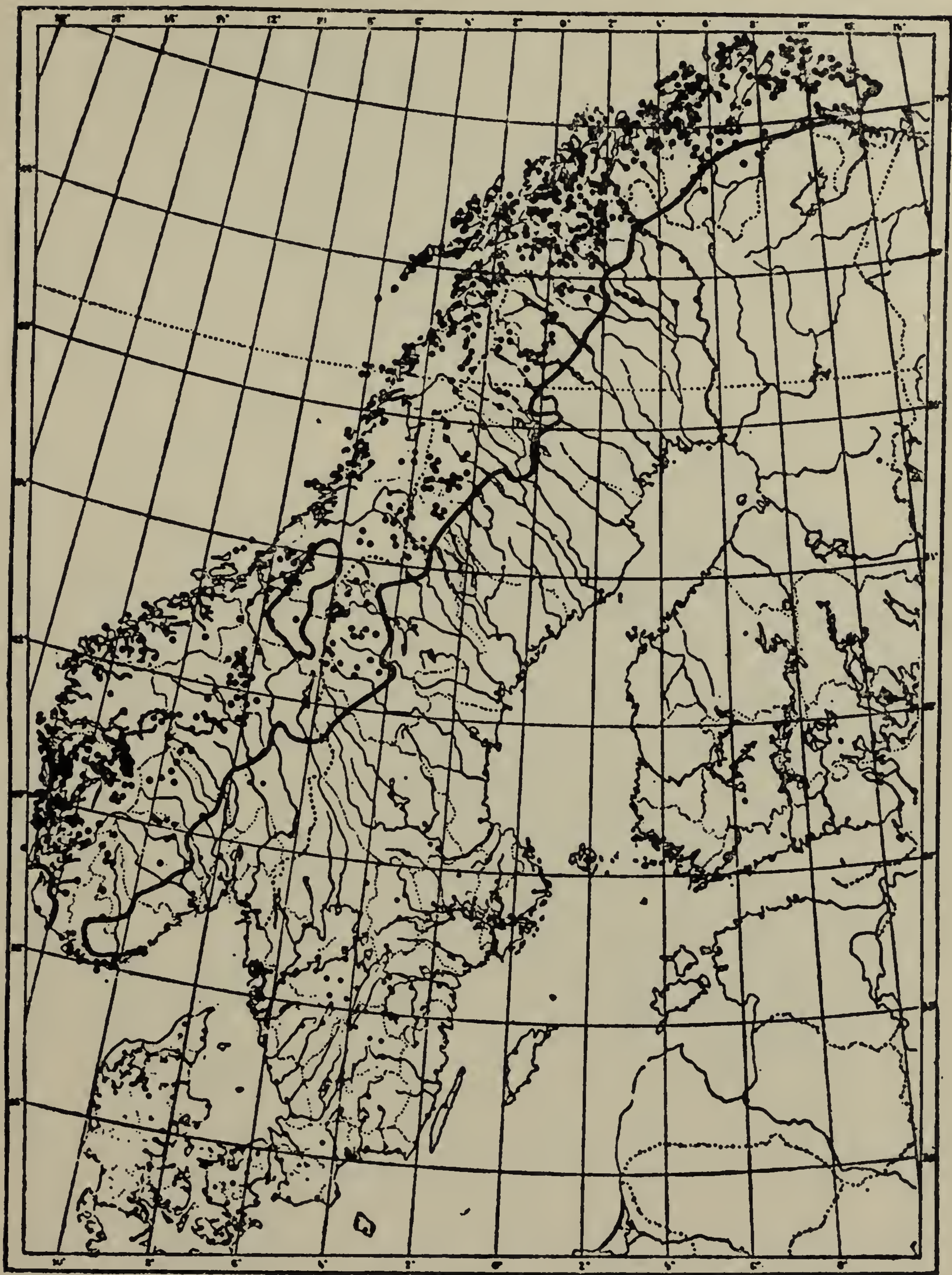

Fig. 3.

The Scandinavian distribution of *Sedum Rosea* (L.) Scop., according to Lid & Zachau, with the 25° C. isotherm.

The strength of these arguments depends upon a detailed correspondence between the distribution limits and the isotherms. A very detailed mapping is, therefore, essential and any filling out of areas, especially along the borders, will blur the picture.

Fig. 4.

The present day and subfossil occurrence of *Salix herbacea* L. in Fennoscandia, according to Hultén, with the 26° C. isotherm. Shaded: Areas where *S. herbacea* is common. Dots: Outlying localities. Rings and crosses: Subfossil late-glacial finds.

In the next example (fig. 4), the distribution of *Salix herbacea* L. is compared with the 26° C. isotherm. In some outlying localities the plants are washed down from the mountains by the rivers and form hardy permanent colonies. Also the occurrence of *Salix herbacea* in Late-glacial and Post-glacial beds outside its present range is entered. In South Scandinavia such finds are

confined to Denmark and the adjacent parts of Sweden. This is a character it shares with other species, e.g., *Salix reticulata.*

While the regional distribution of *Salix herbacea* can be understood in terms of climate alone, this cannot be done in the case of *Salix reticulata* L., which is a calcicole species. Its absence from large areas of the South Scandinavian mountains (see fig. 5) is indubitably due to dominance of archaean rocks giving no suitable soil for the species. Allowing for this the distribution corresponds fairly well with the 26° C. isotherm.

Fig. 5.

The present day and subfossil occurrence of *Salix reticulata* L. in Fennoscandia, according to Hultén, with the 26° C. isotherm. Shaded, Areas where *S. reticulata* is common. Dots: Outlying localities. Rings: Subfossil late-glacial finds.

Fig. 6.

The present day and late-glacial occurrence of *Dryas octopetala* L. in Fennoscandia, according to Hultén, with the 27° C. isotherm. Shaded : Areas where *Dryas* is common. Dots : Outlying localities. Rings : Subfossil late-glacial finds.

Dryas octopetala L. (see fig. 6) is a still more calcicole species than *Salix reticulata*, hence the restriction of range due to edaphic factors is still more marked. In some areas it has a wider distribution than *Salix herbacea* and *reticulata*, it has a wide range in North Finland and goes down to the lower mountains and the sea in South-east Norway. The distribution corresponds fairly well with the 27° C. isotherm.

In contradistinction to *Salix herbacea* and *S. reticulata*, subfossil *Dryas* has been found in numerous places north of Scania and also on the Baltic coast.

Botanists have for some time been aware that finds of real arctic-alpine species in Late-glacial beds are restricted to southernmost Sweden and Denmark. Besides the two *Salices*, this applies to *Diapensia lapponica, Silene acaulis, Saxifraga oppositifolia* and *Ranunculus hyperboreus*. Farther north only *Dryas, Betula nana* and *Arctostaphylos alpinus* have been found, and north of the Middle Swedish Moraines (running from the outer Oslofjord across Sweden to Stockholm) *Dryas* is absent, the characteristic Late-glacial fossil being *Hippophaë*.

All the available facts are consistent with an hypothesis that the summer temperature rose to between 26 and 27 degrees centigrade when the ice withdrew from the areas north of Scania. Such high summer temperatures must have been combined with a rapid retreat of the ice, and geologists have found a rate of retreat of 100-150 m. per year when the ice withdrew north of Scania. North of the Middle Swedish Moraines the figure is still higher.

Most geologists agree that the Middle Swedish Moraines correspond to the climatic deterioration during the Younger Dryas Period, corresponding to zone III in Britain. The rapid retreat of the ice north of Scania would then correspond to the Allerød period (zone II in Britain). It is likely that species with delimiting isotherm substantially lower than 26° C. would have a very bad time and probably become extinct during this period. This is a point of importance in connection with the problem of the origin of the Scandinavian alpine flora.

It is likely that similar patterns will be found by the study of British Late-glacial plants. The abundance of *Salix herbacea* in Late-glacial beds of Ireland, its presence in Cornwall and in north Great Britain but its apparent absence in south-east England may perhaps be explained in a similar way. But more investigations are needed to substantiate this.

I am indebted to the British Council for the opportunity to be present at this meeting.

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GLACIAL RELICS IN THE NETHERLANDS

Dr. Ch. H. Andreas (Groningen).

The changing of a flora may mean two different things. In the first place it may mean a geographic, a visual change—just as we say that a landscape changes during a train journey, let us say from south to north. In the second place it may mean a historical change, the change of a landscape or a flora in the course of years, as to which we may consider the few years of a man's lifetime as well as the geological periods of thousands and millions of years. In speaking about glacial relics of the Netherlands, I shall restrict myself to the last mentioned historical changing of the flora.

I need not go into details on the various shiftings of the ice-sheets in earlier periods, nor need I explain the term "glacial relics", which in botany covers plants of an ordinary arctic, northern and perhaps alpine distribution, which, preceding the ice, came down from their ordinary area and which stayed in some of the new localities after the retreat of the ice. Those plants are characterized by a so-called disjunct area; they are of a local occurrence and do not spread actively, though there may be some spreading in consequence of more recent changes of climatic and edaphic conditions.

During the third of the four glacial periods, the so-called Riss-period, the northern half of the Netherlands was actually covered with ice, which had its southern borderline running from Amsterdam to Utrecht and further down to the south-east. We shall not deal with this period to-day, though the climate may have been not too bad and there may have existed some vegetation at that time.

But also the Würm-period, when the ice did not reach further than southern Sweden, had its indirect influence on the flora of the Netherlands; fossil remains of plants of a tundra-vegetation of that time have been found in the eastern part of the country, plants such as *Salix herbacea, S. polaris, S. reticulata, Betula nana, Arctostaphylos Uva-ursi, Dryas octopetala* and *Selaginella*. They went back to their northern stations along with the ice.

Yet some plants are likely to have remained in their Dutch localities; we may instance *Cornus suecica, Linnaea borealis, Trientalis europaea,* perhaps *Arctostaphylos Uva-ursi* and *Rubus saxatilis* and perhaps *Scheuchzeria palustris, Carex limosa* and *Eriophorum vaginatum* of the eastern Sphagnum-bogs. Probably there is one more species, *Carex aquatilis,* with which however we shall deal later on. We usually consider these plants, especially *Cornus, Linnaea* and *Trientalis,* as glacial relics in the Netherlands; but there is a difference of opinion about their

status as such between Dutch botanists in connection with the fact that our country lies in the route of migratory birds which migrate in autumn from Scandinavia and the Baltic to the south, such as species of the genera *Corvus* (crows) and *Turdus* (thrushes) for example (Fig. 7).

Fig. 7.

Map of distribution in the Netherlands of *Cornus suecica* ●, *Linnaea borealis* ■ *Trientalis europaea* ▲, *Carex aquatilis* + (present localities) and × (fossil remains). The lines are three out of many, demonstrating routes of migration of the song thrush (*Turdus e. ericetorum*).

Cornus suecica and *Linnaea borealis* grow locally on diluvial grounds in the northern provinces of the Netherlands, but their area is not clearly disjunct. Between the Scandinavian and the Dutch region there are known scattered localities in Denmark and in north-west Germany respectively, which lie on the route of those migratory birds which are berry eaters, in autumn at least. And as the fruits of both species are berries, the late Professor Weevers presumed a transport of the fruits by those birds and consequently a more or less recent settlement (or resettlement) of *Cornus* and *Linnaea* in the Netherlands, where they sometimes occur in historically young vegetation. For this reason he proposes to call these plants pseudo-relics, not relics. The same may hold good for *Arctostaphylos Uva-ursi,* growing on the isle of Terschelling and in one place in the centre of the country.

Trientalis was known from the east and north-east of the Netherlands and within the last 30 years it was also discovered on two of our North Sea islands, Terschelling and Vlieland. The theory of a transport of its capsules together with earth on the feet of birds at least to the Dutch isles is less attractive than that by the berry eating birds in the case of *Cornus, Linnaea* and perhaps of *Arctostaphylos.* Yet the occurrence of *Linnaea* in a fairly young vegetation of pine-woods is not necessarily an objection against its position as a glacial relic. For glacial relics need not have been constant as to their localities from glacial times up to the present, provided there were always suitable growing conditions available. There will have been little migration from one place to another.

Only the aid of an uninterrupted series of fossil remains will enable us to decide in favour of the relics. *Betula nana* in the German Erzgebirge gives a most striking example of such a series.

We now turn to *Carex aquatilis,* a plant which has been found in the Netherlands two or three times during the last hundred years. But the specimens had not been recognized as such for in the herbarium they had been erroneously named *Carex acuta* or *Carex gracilis.* They were recognized only recently by three Dutch field botanists who predicted its present occurrence in the north of our country. And, indeed, one year after their prediction, in May 1948, one of my colleagues and I rediscovered *Carex aquatilis,* growing in a pool in the same village where it had been found in 1845; we do not know whether it was exactly the same locality. Afterwards we also found the plant in the province of Drente, while the Natural History Club of Groningen discovered a small but very abundant colony near to the abovementioned station in 1951.

Carex aquatilis most resembles *Carex gracilis,* from which it differs however by its blunt-edged stalk, its very long lowest bract which is considerably longer than the inflorescence, by the turning upwards of its drying leaves (*Carex gracilis* turns downwards)

and by its pale green nerveless utricles. The base of the stem is purplish and the leaf-tips are bluish-grey.

Now I consider *Carex aquatilis* as another glacial relic of the Netherlands. It is an arctic-subarctic plant of circumpolar distribution. Its occurrence in the Netherlands means a disjunction, for *Carex aquatilis* has not yet been found in Germany or in Denmark, and there is a distance of about 700 kilometres between the Dutch and the Swedish stations. The distribution in Europe can be seen on the map. I am not certain about Iceland, where Dr. Löve, who knows its flora well, denied the presence of *Carex aquatilis,* but its occurrence in Iceland is mentioned in botanical literature. Yet this uncertainty cannot influence my opinion.

The questions which remain are whether the plant grew in our country in the Pleistocene and, secondly, has it found suitable circumstances for its growth ever since?

The first question can be answered in the affirmative. Fossil remains of *Carex aquatilis* were found in the east of our country (Hengelo) in the tundra-flora of the Würm-glacial period mentioned before, together with such plants as *Dryas octopetala* and *Salix reticulata.* Moreover, it was found in a lock-chamber near Wijk bij Duurstede in a layer of clay of the Late-glacial period and it is remarkable that with it the fossil remains were found of plants which grow together with *Carex aquatilis* in its present habitats:—*Betula, Salix, Alisma, Carex, Comarum, Eleocharis, Filipendula, Mentha, Menyanthes, Nymphaea, Oenanthe, Ranunculus* (*Batrachium* included), *Sparganium.*

Moreover a very rich Late-glacial vegetation of *Carex aquatilis* was found in Germany, together with *Betula nana.*

It will be difficult to trace whether *Carex aquatilis* has been able to stand climatic conditions, that is to say temporarily different combinations of many factors ever since the Pleistocene, but *Betula nana* in Germany is a proof that there is at least one plant able to do so. And why should not there be more?

Palaeobotanical investigations in the Netherlands have shown already that stagnant water, probably the chief requisite for *Carex aquatilis,* has been present on boulder clay in the province of Drente ever since the end of the Pleistocene. And its present occurrence in old riverbeds points to the possibility of the tiding over in such places in certain climatic periods, such as the Atlantic with its decreasing number of open pools and a development of Sphagnum bogs which made the struggle for life more difficult for *Carex aquatilis.*

As far as I know from a distribution map, kindly procured me by Mr. Nelmes of Kew Herbarium, *Carex aquatilis* occurs in Wales, northern England and Scotland. To my knowledge it has not yet been found in the famous Teesdale region. In Ireland it grows together with *Carex rigida,* with which it may be

confused in the fossil state. Yet the remains of *Carex aquatilis* do not seem to be the most difficult to be distinguished within the genus.

I hope that palaeobotanists in my country will pay attention to the species and find an uninterrupted series of fossil remains from the Pleistocene up to the present time, by which they would strongly support my hypothesis that *Carex aquatilis* is a glacial relic in the Netherlands.

I wish to express my thanks for the kind invitation from your Society, and for the aid of the British Council, which enabled me to attend your conference and join your excursion, and to contribute this communication.

This paper was discussed as follows:—

Dr. Walters said that *Carex aquatilis* Wahlb. was now known from Teesdale. He had recently seen it near Middleton.

Mr. Meikle stated that a colony of *Carex aquatilis* grows by the side of the reservoir at Glenasmole, Bohernabreena, Co. Dublin. This is an artificial habitat, and the sedge is not known to occur as a native elsewhere in the vicinity. It has been flourishing at Glenasmole for many years, and its origin remains unexplained.

SOME PARALLELS BETWEEN THE BRITISH AND SCANDINAVIAN MOUNTAIN FLORAS

(Exhibit)

A. MELDERIS.

A selection of specimens, as well as some maps showing their distribution, was exhibited to illustrate the close relationship between the British and Scandinavian mountain floras.

As regards the geographical distribution, the mountain plants common to both floras can be divided into three general groups.

The first group, which corresponds to the Arctic-subarctic element of Matthews (1937), contains about 37 exclusively northern species, not extending to the mountains of Central and S. Europe.

Nearly half of them (about 16) belong to the boreo-atlantic species which are distributed in N. Britain and Scandinavia (in some instances also in Spitzbergen and Novaya Zemlya), reaching sometimes the Faeroes, Iceland, S.E. Greenland and eastern N. America. Several species have amphi-atlantic distribution, being confined to the two sides of the North Atlantic Ocean (cf. Hultén, 1950). Thus, *Cerastium Edmondstonii* (Edmondst.) Murb. & Ostf., *Draba norvegica* Gunn. (*D. rupestris* R. Br.), *Euphrasia frigida* Pugsley*, *Erigeron borealis* (Vierh.) Simm., *Festuca vivipara* (L.) Sm., and *Carex recta* Boott extend to N. America. *Poa flexuosa* Sm. (not found in the Faeroes) reaches Greenland. Its hybrid with *P. alpina* f. *vivipara* L. (*P.* × *jemtlandica* (Almq.) Richt.) is found in Scandinavia, Scotland and Iceland. *Alchemilla Wichurae* (Bus.) Stefansson seems to have the same range as *P. flexuosa,* but it is met with also in the Faeroes. The plant recorded from a locality in Riesengebirge probably belongs to alpine *A. connivens* Bus. which is closely related to *A. Wichurae*. *Arenaria norvegica* Gunn., formerly referred to *A. ciliata* L. (growing in the Pyrenees, Alps and Carpathians), reaches Iceland, but has not been found in the Faeroes as yet. (Fig. 8). *Euphrasia scotica* Wettst. extends to the Faeroes. The following species are so far recorded only from N. Britain and Scandinavia: *Hieracium reticulatum* Lindeb., *H. stictophyllum* Dahlst. and *H. argenteum* Fr., *Carex Grahami* Boott and *Orchis purpurella* T. & T. A. Steph.

* Callen (1952) has regarded *E. frigida* and *E. eurycarpa* Pugsley as varieties of *E. arctica* Lge. (*E. Marshallii* Pugsley), the first as var. *obtusata* (E. Joerg.) Callen and the second as var. *submollis* (E. Joerg.) Callen (distributed in Norway, Scotland, Iceland, Greenland and Canada). The British species of *Euphrasia* are in need of further critical revision.

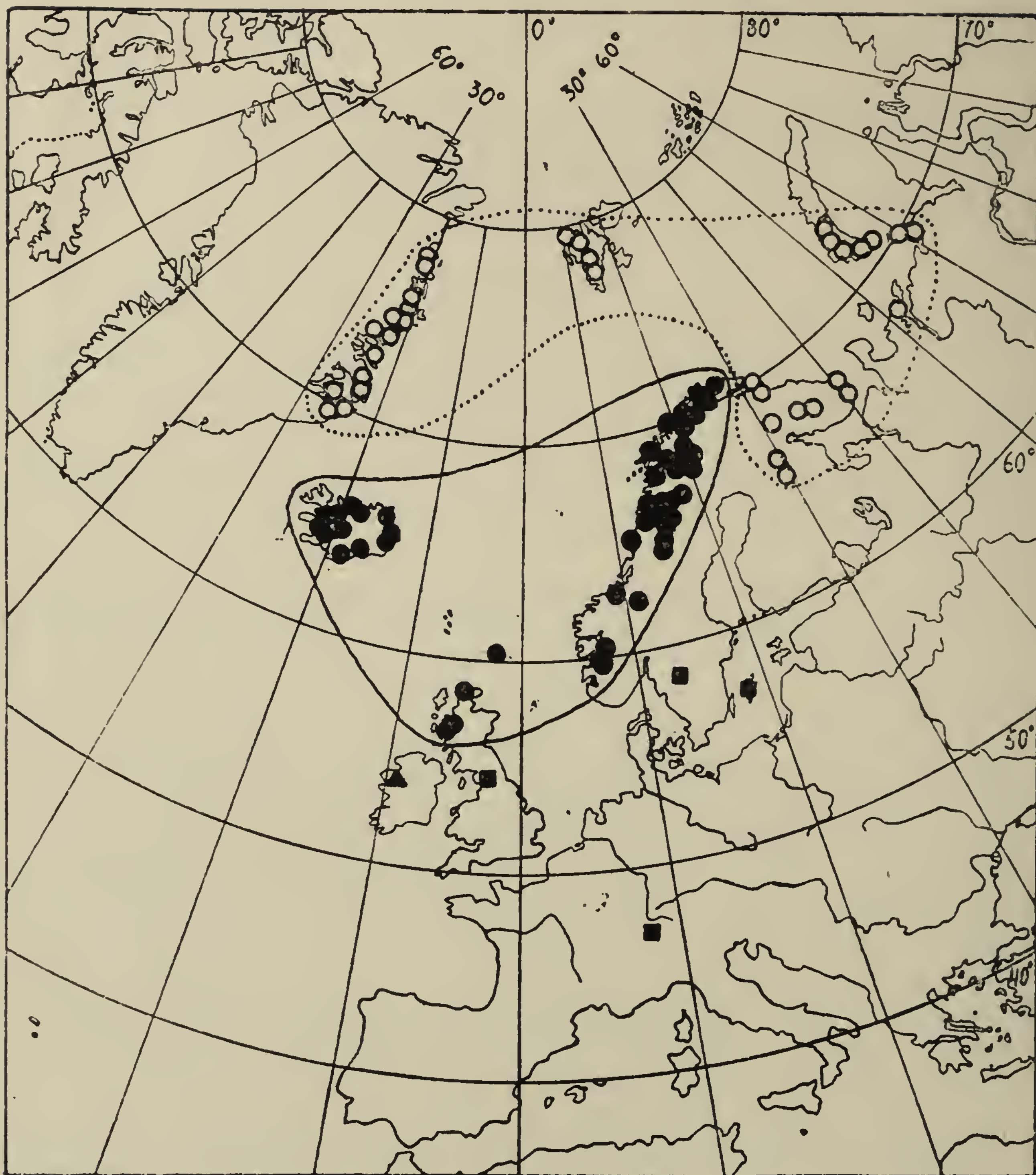

Fig. 8.

The distribution of *Arenaria norvegica* Gunn. (●), *A. gothica* Fr. (■), *A. ciliata* ssp. *hibernica* Ostf. & Dahl (▲) and of *A. ciliata* ssp. *pseudofrigida* Ostf. & Dahl (○).

The other species of the first group (about 21) are widespread in the arctic, subarctic and montane regions of the northern hemisphere and most of them have a circumpolar distribution, e.g., *Koenigia islandica* L. (found in the Isle of Skye), *Sagina intermedia* Fenzl, *Minuartia rubella* (Wahlenb.) Hiern, *Saxifraga rivularis* L., *S. caespitosa* L. (Fig. 9), *Diapensia lapponica* L. (recorded from Glenfinnan in Inverness), *Poa pratensis* ssp. *alpigena* (Fr.) Hiit., *Poa glauca* Vahl, *Eriophorum brachyantherum* Trautv. [*E. opacum* (Björnstr.) Fern.], *Carex saxatilis* L., *C. rariflora* (Wahlenb.) Sm. and *Luzula arcuata* Sw.

The second group, which includes the Arctic-alpine element of Matthews, comprises more than 80 species, the general range of which lies in the arctic or subarctic regions and reappears farther south in the mountains of Central and S. Europe. The majority of them, e.g., *Salix reticulata* L., *Viscaria alpina* (L.) Don, *Dryas octopetala* L., *Potentilla Crantzii* (Cr.) G. Beck, *Loiseleuria procumbens* (L.) Desv. and *Gnaphalium supinum* L., occur also in the mountains of Asia and/or America. Some species of this group have also amphi-atlantic distribution, similar to that of the first group. Thus, e.g., the range of *Alchemilla alpina* L. and *Veronica fruticans* Jacq. extends to Greenland, but that of *Salix herbacea* L., *Cerastium alpinum* L., *Saxifraga stellaris* L., *Alchemilla glomerulans* Bus. and *A. filicaulis* Bus. reaches eastern N. America.

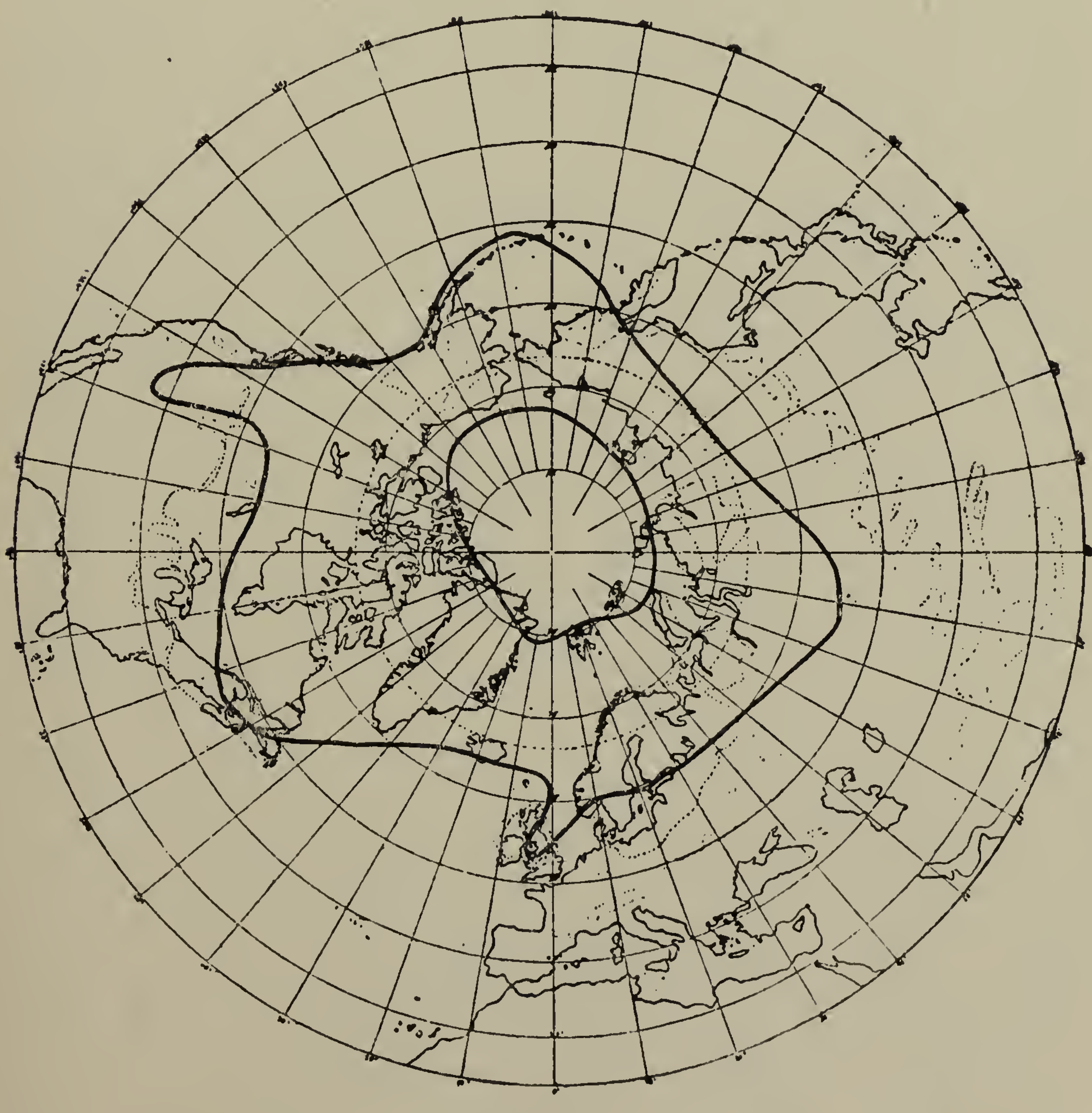

Fig. 9.

The distribution of *Saxifraga caespitosa* L., after Löve & Löve (1951).

Judging from the climatic and soil requirements these groups include species having a suboceanic, sub- or low-arctic range (cf. Böcher, 1951). The typical high-arctic plants growing in continental climatic conditions do not occur in the British Isles, but they are represented in the N. Scandinavian mountains where they have occupied situations corresponding to continental tundra. Some of them, termed west-arctic, such as *Arenaria ciliata* ssp. *pseudofrigida* Ostf. & Dahl (Fig. 8), *A. humifusa* (Wahlenb.), *Stellaria crassipes* Hultén, *Potentilla Chamissonis* Hultén, *Poa arctica* var. *caespitans* (Simm.) Nannf. and *Carex holostoma* Drej., have also an amphi-atlantic distribution, but in contrast to the above-mentioned species they occur in higher latitudes. In addition, the Asiatic element enriches still more the Scandinavian mountain flora.

The third group of the species common to the British and Scandinavian mountain floras is represented by the ubiquitous element, occurring both in the lowlands and highlands, e.g. *Trollius europaeus* L., *Anthyllis Vulneraria* L., *Vaccinium Myrtillus* L., *Campanula rotundifolia* L., *Solidago Virgaurea* L. and *Festuca ovina* L. In many cases these species have developed peculiar montane biotypes.

The distribution of the plants belonging to the first two groups gives a valuable indication of the age and origin of the floras in question. Their geographical areas are discontinuous. It is very difficult to explain the occurrence of these species in their present situations separated by the broad seas and oceans, especially with regard to the Faeroes, Iceland and Greenland, if we accept the view of older authors, e.g. Nathorst (1891) and Ostenfeld (1901). According to them, the vegetation of the countries in question, as well as in northern Europe, had been destroyed by a great ice-sheet during the Ice Age. The arctophilous species could have survived at the margin of the glaciers. These authors assumed that present vegetation could have arrived there at the end of the Ice Age after the retreat of the glaciers, travelling from more southern or eastern regions over a big land bridge. Modern students of the arctic flora, as well as the geologists, nevertheless deny the presence of such land connexion in the post-glacial period. If the connexion existed, the disappearance of it must have taken place much earlier. In that case the plants could have arrived in the isolated countries only by the aid of birds, air, sea-currents and man, but we have no evidence at present that these means could have played an important rôle in the dispersal of the montane species. Thus, according to A. & D. Löve (1951, p. 394), of all (about 585) higher plants in Iceland, "not more than 30 per cent have been introduced in historical times, not more than 15 per cent might have dispersed by aid of mainly sea-currents in post-glacial and pre-historical times . . .".

At the end of the last century Blytt (1893) showed that the "extinction" theory cannot explain the occurrence of some N. American and Greenland plants in Scandinavia. The absence of

them on the European continent and in Siberia excluded their immigration from the south and east. Blytt considered them as relicts of an interglacial flora, which had survived one or more glaciations there. Later he assumed that these western plants had immigrated to Scandinavia before the last glacial period over a transatlantic bridge connecting Greenland, Iceland, the Faeroes, Scotland and W. Norway. His ideas of the survival of the plants in Scandinavia during the Ice Age, supported also by Sernander (1896) and Hansen (1904), were substantiated by Th. E. Fries (1913) in a detailed "over-wintering" theory, which was based on a distribution of the mountain species (in all 140) in Scandinavia and in other countries, as well as on some geological facts. Since the publication of this theory extensive research work has been done by Scandinavian botanists, dealing with the distribution, taxonomy and cytology of the mountain plants. In many cases, it has been proved that Scandinavian plants, which formerly were identified with species occurring on the mountains of Central Europe, differ from them, e.g. *Arenaria norvegica, Euphrasia lapponica* Th. Fr. and *Poa flexuosa*. These discoveries give a valuable indication in favour of the survival of the plants in Scandinavia (cf. Nordhagen, 1935; Nannfeldt, 1935, 1947; Selander, 1950, etc.).

The studies of the distribution of the mountain plants in Scandinavia revealed also that they occupy two separate areas. One of these areas is situated in the mountains of S. Norway, where several endemic forms, such as *Papaver relictum* (Lundstr.) Nordh., *Draba cacuminum* E. Ekm., *Poa arctica* var. *stricta* (Lindeb.) Nannf., etc., have been recorded. Also the majority of the boreo-atlantic species common to the Scandinavian and British floras occur there. As they could immigrate neither from the south nor the east, it has been assured that they may have survived in some ice-free refuges, when the Ice Age was at its maximum. From the distribution of these plants, it has been possible to determine somewhat accurately the locations of the refuges, which seem to be localised on or near the sea-shores (in Vaage-Lom-Lesja District and in Dovre). The other area is confined to the northern part of Scandinavia (from Salten to W. Finmark and Torneträsk District in Swedish Lapland). It is occupied also by many interesting plants, such as west-arctic species and several endemic forms, e.g. *Papaver Laestadianum* Nordh., *P. lapponicum* (Tolm.) Nordh., *Taraxacum tornense* Th. Fr., *Poa arctica* var. *tromsensis* Nannf. and var. *microglumis* Nannf. These species together with others may have found some refuges in the same area, near the sea-shore and on some "nunataks". Several Scandinavian plants, e.g. *Saxifraga hieraciifolia* Waldst. & Kit., *Rhododendron lapponicum* (L.) Wahlenb., *Campanula uniflora* L., *Carex arctogena* H. Sm. and *Luzula parviflora* (Ehrh.) Desv., have "bicentric" distribution, being distributed in both areas. The discontinuity of the range of these plants is explained generally as a result of the survival of them in two different parts of

Scandinavia. Böcher has assumed that this discontinuity may have been caused by climatic and edaphic conditions.

M. Fries (1949) has expressed an opinion that numerous arctic-alpine as well as many subalpine plants have survived in different refuges, scattered along the sea coast. From the sheltered stations the survivors could spread inland after the melting of the ice. Now they occupy those situations on the mountains where the environmental conditions are most suitable for them (cf. Böcher).

It can be accepted that not only herbaceous plants could have survived in refuges, but also trees and shrubs. According to Nannfeldt (1947), *Betula callosa* Notö (found also in Iceland) and other mountain birches, willows, *Myricaria germanica* (L.) Desv., etc., may be glacial survivors. In western Jämtland the remains of *Hippophaë rhamnoides* L. have been found in the deposits of the late glacial period, and Nannfeldt assumes that it could have survived in a refuge in Norway. This plant in southern Sweden seems, however, to be an immigrant in the early post-glacial epoch.

When the floras of the other boreal regions were more completely studied, a number of rare species as well as endemic forms were found in or near the situations which later have been recognized by geologists as never having been glaciated. Thus, Fernald (1925) showed that numerous species in boreal N. America (in St. Lawrence region) have survived the Ice Age. Warming (1888, 1891), Gelting (1934), etc., have given the reasons for believing that ice-free shelters also existed in Greenland. Hadac (1948), A. & D. Löve (1947, 1951), etc., have accepted the existence of refuges in Iceland. The presence of many species, especially boreo-atlantic, in the Faeroes could be explained by the assumption that they are survivors of the Ice Age (cf. Warming, 1902-3).

As regards the origin of the mountain flora of the British Isles, the considerable number of the species (about 37) common to the British and Scandinavian mountains, but not occurring in those of Central and S. Europe, is in favour of the close relationship between the two floras. This statement is in agreement with Wilmott's (1930) and Matthews' views that the British mountain species are of Scandinavian affinity.

It is very difficult to explain the occurrence of many of the above-mentioned species in Britain, especially those which in Scandinavia and other countries have been regarded as pre-glacial relicts. They could not immigrate there from Scandinavia or other boreal countries in the post-glacial period, because the British Isles had no land-connexions with these countries at that time. The remains of these plants have been found neither in deposits of the pre-glacial period in the unglaciated part of Britain (to the south of a line joining the Severn and the Thames) nor on the other side of the Channel. If the ice-free shelters existed in Greenland, which has been considered as the actual centre of the

northern ice-sheet, when the glaciation was at its maximum, then it is evident that they should have been also to the north of the Thames.

The existence of such unglaciated areas has been recognized by many authors here. Thus Wright (1914) showed that considerable areas of the Pennines and Yorkshire show no signs of ever having been covered by ice. His view was supported by Wilmott (1930, 1935), who pointed out that Upper Teesdale in the Pennines is remarkable for the number of rare plants occurring there to-day, e.g., *Viola rupestris* Schmidt, *Minuartia stricta* (Sw.) Hiern (neither is found elsewhere in the British Isles), *Myosotis alpestris* Schmidt, *Dryas octopetala* L., *Gentiana verna* L., *Potentilla fruticosa* L., as well as some southern species, such as *Senecio spathulifolius* Turcz., *Helianthemum canum* (L.) Baumg., etc. According to him, these plants are survivors which had found a shelter in that station during the Ice Age. T. W. Woodhead (1924) regarded the heath vegetation of the Pennines as being of pre-glacial origin. As shown by Dandy and Taylor (1946), the occurrence of *Potamogeton* × *suecicus* Richt. in Yorkshire (in the rivers Ure and Wharfe) and in the river Tweed, outside the present area of one parent (*P. filiformis* Pers.) and only rarely in association with the other (*P. pectinatus* L.), indicates that it also may be a glacial relict which has survived in the given localities.

Wilmott considered that flat-topped mountains, which are characterized by rare plants to-day, have proved to be refuges. According to him (1935), there had also been refugees on the following mountains: on Ben Bulben (in Ireland), which has *Arenaria ciliata* L. (regarded by Ostenfeld & Dahl as an endemic subspecies—ssp. *hibernica* (Fig. 8)), *Polygala vulgaris* var. *grandiflora* Bab. [resembles var. *Ballii* (Nym.) Ostf., found only in the Faeroes] and a peculiar form of *Thalictrum minus* L.; on Ingleborough (in Yorkshire) with *Poa alpina* L. and *Arenaria gothica* Fr. (Fig. 8), which has a striking discontinuous area, being found outside this locality only in Gotland and Västergötland (Sweden) and in Switzerland; and in the Cross Fell area where *Myosotis brevifolia* C. E. Salmon (an endemic species) occurs.

Also the Snowdon area (Caernarvon) includes some plants, e.g., *Cerastium Edmondstonii, Saxifraga caespitosa, Poa alpina* f. *vivipara* L., *P. glauca* and *Lloydia serotina* (L.) Rchb., the ranges of which give an indication that they may be relicts from preglacial and glacial times. It is interesting to note that *Lloydia serotina* does not occur in Scandinavia, but it has a striking discontinuous circumpolar range [see the maps of the distribution given by N. Woodhead, 1933, 1951].

Much attention has been directed also to the flora of the Western Isles of Scotland (the Inner and Outer Hebrides, including St. Kilda), which are of considerable phytogeographical interest to students of the origin and history of the British flora, as shown by Turrill (1948) and J. Heslop Harrison (1948). Among

the plants having a wide distribution in the British Isles, there are to be found many arctic-montane species, such as *Cardaminopsis petraea* (L.) Hiit., *Silene acaulis* (L.) Jacq., *Oxyria digyna* (L.) Hill, *Polygonum viviparum* L., *Deschampsia alpina* (L.) Roem. & Schult., etc., which often, as in Scotland, grow near sea-level, as well as some very local plants in the British Isles, e.g., *Juncus pygmaeus* Rich. (Lizard), *J. capitatus* Weig. (Land's End, Lizard, Anglesey, Channel Islands) and *Exaculum pusillum* (Lam.) Caruel (cf. Turrill, 1948). There occur also several endemic forms in the genera *Orchis, Euphrasia,* and *Hieracium.* The distribution of these plants indicates that some of them may be relicts of the pre-glacial flora. Also the occurrence of several American species having a restricted distribution in the British Isles is in favour of the assumption that many islands of the Inner and Outer Hebrides were unglaciated. They are: *Eriocaulon septangulare* With., found in Skye and Coll (also in Ireland, from W. Cork to W. Donegal), *Spiranthes Romanzoffiana* ssp. *stricta* (Sm.) Clapham, occurring in Colonsay and Coll (elsewhere in Ireland, from Lough Neagh in Londonderry, Antrim, Down and Armagh) and *Potamogeton epihydrus* Raf., recently discovered as a native in S. Uist in the Outer Hebrides (J. W. Heslop Harrison, 1949; Taylor, 1949).

One of the interesting islands of the Hebrides in connexion with the composition of the flora is Rhum in the Inner Hebrides, which seems never to have been glaciated. Some rare plants occur there, e.g. *Arenaria norvegica* Gunn. (known also from two localities in W. Scotland and in one in Shetland), *Thlaspi calaminare* Lej. & Court. (known also from Matlock and other localities in Derby), some very puzzling mossy saxifrages, and *Euphrasia Heslop-Harrisonii* Pugsley (elsewhere known only from W. Ross), as well as several endemic forms, such as *Orchis Fuchsii* ssp. *rhumensis* Heslop-Harrison f., *Euphrasia rhumica* Pugsley, etc.*

According to Turrill (1928) the isolated islands of St. Kilda also were not covered by an ice-sheet. In his study on the flora of these islands, he came to the conclusion that the main mass of the heath-moor vegetation had survived the Ice Age in the St. Kilda group. In his opinion at least five species might be woodland relicts.

As regards the Shetland Islands, it is found that Foula was partly covered by an ice-sheet, and a part of its vegetation may have survived there, as shown by Turrill (1929).

The bulk of the plants common to the mountain floras of the British Isles and Scandinavia are distributed in Scotland. In addition, there occur several plants with restricted distribution in the Inner and Outer Hebrides and Shetland, as well as some

Carex bicolor All. recorded from the Isle of Rhum seems to be an introduced plant (cf. Raven, 1949). The status of *C. glacialis* Mackenzie as an indigenous plant in Rhum is also doubtful.

endemic forms, e.g. *Calamagrostis scotica* (Druce) Druce (Caithness), *Roegneria Doniana* (F. B. White) Meld. (Ben Lawers and adjacent mountains in Perth and near Inchnadamph in W. Sutherland; (cf. Melderis, 1950; Raven, 1952), *Rhinanthus Lintoni* Wilmott mountains of Dunbarton, Angus and Perth), *R. lochabrensis* Wilmott (Glen Nevis), *Primula scotica* Hook. (W. Sutherland, Caithness and Orkney) and several species of *Hieracium*. The occurrence of *Alopecurus alpinus* Sm. in Scotland (on the higher Scottish mountains from Perth to E. Ross) is of particular interest. This species does not occur in Scandinavia, but it is found in Spitzbergen, Franz Josef Land, Novaya Zemlya, Kolguev, the Urals, N. Asia and N. America, as well as in Greenland, except the southern part (cf. Hultén, 1941). The distribution of this and many other rare plants having a peculiar discontinuous range outside the British Isles seems to indicate that they may have survived the Quaternary Period in Scotland in some sheltered ice-free situations ("nunataks") near the sea coast.

The distributional range of these species in Scotland is insufficiently known at present to determinate the possible locations of the shelters. Intensive studies on the ecology, variability and cyto-genetics of the Scottish plants may reveal many interesting facts concerning the origin and history of the British mountain flora.

The data available to-day, however, lead to the suggestion that many plants seem to have been living in their present situations during the Ice Age, and that they had arrived there at least before the last glaciation (cf. Matthews). Judging from the large element common to N. American and European floras, it seems that there was a connexion (the proximity of the continents, or continuity of arctic lands, or a land-bridge) between these two continents in the North Atlantic, also probably between Scotland and Scandinavia in the past (cf. Nordhagen, 1935).

Different views as to the cause and the manner of disappearance of the connexion are held (cf. Wulff, 1944, 1950). There is also a wide divergence of opinion concerning the time when the separation of the countries may have taken place. Thus according to Thoroddsen (1914) the land connexion might have disappeared in the late Miocene or at least before the beginning of the Ice Age, but according to Hadac during the Würmian period.

The history of the flora since the post-glacial epoch is much better known, owing to investigations of plant remains and pollen grains in the deposits, e.g. in peat-beds (Godwin, 1934).

In his studies on immigration of the flora in Norway, Blytt (1876, 1882a, b) found that climatic conditions in the post-glacial epoch were characterized by alternation of warm and cool periods, which were either wet or dry, each being in turn advantageous to a particular group of plants. Later his theory was definitely established by results obtained by Sernander (1892, 1910), etc., in the investigations of the peat-beds in Sweden. A similar

sequence of successions of the periods and plants has been found also in the British Isles, as shown by T. W. Woodhead (1929), Tansley (1939), Good (1945), etc.

After the melting of the ice-sheet surrounding the shelters, the survivors occupied suitable situations where they mixed with plants following the retreat of the glaciers from the southern regions. When the climate became warmer, the mixed arctic-montane flora migrated northward or to the higher altitudes of the mountains. The localities left free were colonized by woodland elements and thermophilous plants. Further climatic variations caused changes in the species composition of the floras, as well as in the distribution of the species.

Changes in the constitution of the mountain flora are at first influenced by climatic and edaphic factors which determine the distribution of the plants and can advance the origin of new types (modifications or genetically fixed forms). Studies of the mountain plants from the cytogenetic and taxonomic point of view have shown also that processes of evolution, viz. hybridization, polyploidy and mutation, associated with selection, are important in the changes of the vegetational features of the mountain flora.

Hybridity tends to increase the variability in populations by genetical recombination of characters. In many cases it results in destroying the limits between the species, producing intermediate forms. Hybrids are more easily recognized in field populations than in isolated herbarium specimens. Partially sterile hybrids, which have "empty" pollen grains, can produce a very polymorphic and more or less fertile offspring in back-crossing with the parent species, growing together with them in the field, as in *Roegneria canina* × *mutabilis,* observed by me in northern Sweden.

Natural interspecific hybrids have been found in many genera of the mountain plants of both the British Isles and Scandinavia. In the British flora hybrids commonly occur in the genera *Salix, Epilobium, Euphrasia* and *Carex* (cf. Clapham, Tutin & Warburg, 1952). They are met with also in *Cerastium* (*C. alpinum* × *vulgatum*), *Cochlearia* (*C. officinalis* × *scotica*), *Saxifraga* (*S. nivalis* × *stellaris, S. hypnoides* × *tridactylites, S. hirsuta* × *spathularis,* the latter of which does not occur in Scandinavia), *Poa* (*P.* × *jemtlandica* = *P. alpina* f. *vivipara* × *flexuosa*) etc. Several species have been regarded as having a hybrid origin, e.g. *Orchis Francis-Drucei* Wilmott (a hybrid derived from *O. purpurella* T. & T. A. Steph. and *O. ericetorum* (E. F. Linton) E. S. Marshall), *Rhinanthus Lintoni* and *R. lochabrensis* (probably offsprings of crossings between *R. borealis* (Stern.) Druce and *R. stenophyllus* (Schur.) Druce or *R. spadiceus* Wilmott). In comparison with the Scandinavian flora, it is poorer in hybrids, but this can be explained by the fact that the Scandinavian mountain flora is richer in species, many of which have been much more fully investigated from the cytogenetic point of view.

The role of hybridization, combined with gametophytic apomixis, in the origin of forms has been clearly demonstrated by Nygren (1950a, b) in his study on the species of *Poa*, occurring in the Scandinavian mountains. According to him, numerous forms of *Poa* have arisen in crossing between apomictic, facultative sexual and sexual types. Some of them can propagate only by vegetative means, while others may produce new forms by crossing. Nygren (1950a, p. 232) mentions: "In this way the number of forms increases every year, provided that the outer conditions do not change".

It seems that the polymorphy of some apomictic groups in the mountain flora of the British Isles has arisen in the same way. Apomixis has been stated to occur in many genera, such as *Alchemilla, Potentilla, Taraxacum, Agrostis, Calamagrostis, Deschampsia, Poa, Festuca,* etc. (cf. Gustafsson, 1946, 1947a, b).

A striking feature of the mountain flora is the occurrence of vivipary (replacing of flowers and spikelets by bulbils), which is more frequent in the Arctic flora. In the British mountain flora the vivipary occurs in *Polygonum viviparum* L., *Saxifraga cernua* L., *Poa alpina* f. *vivipara* L., *P.* × *jemtlandica* (Almq.) Richt., *Festuca vivipara* (L.) Sm.*, *Deschampsia alpina* (L.) Roem & Schult. and *D. caespitosa* (L.) Beauv. The same plants grow also in Scandinavia, but there viviparous forms are found also in some other species, such as *Poa pratensis* L. *s. lat., P. arctica* R.Br. (not occurring in Britain) as well as in a hybrid *P.* × *herjedalica* H. Sm. (*P. alpina* f. *vivipara* × *pratensis* ssp. *alpigena*) and *Festuca rubra* L. (cf. Nannfeldt, 1940). From the genetic point of view these viviparous plants may be comparable to the obligate apomicts, as pointed out by Stebbins (1950).

Nannfeldt (1937, 1940) has shown that vivipary in *Poa* and in other grasses is a consequence neither of modification nor of hybridization. According to him, the ability to transform the spikelets into bulbils is genetically fixed and associated with environmental conditions. As shown by Müntzing (1940), some viviparous clones of Swiss *Poa alpina* may have originated by mutation from non-viviparous biotypes having the same chromosome number and growing in the same locality.

As to the abundance and distribution of these forms, Nannfeldt (1940, p. 32) has mentioned that "Non-viviparous biotypes are as a rule both more common and more widely distributed

*Wilmott (1945) in his studies on *F. vivipara* from Uig (in the Outer Hebrides) has found that it is heterogeneous there. Some forms seem to be identical with ssp. *faeroensis* (Turesson) Wilmott and ssp. *vaagensis* (Turesson) Wilmott, which is said by Turesson (1926-7) to be distributed in the Faeroes and Iceland. Some others show a close resemblance with ssp. *jemtlandica* (Turesson) Wilmott, which, according to Turesson, is known from the Norwegian coast. In addition to them Wilmott has described ssp. *uigensis* known only from Uig. In the Scottish material of *F. ovina* Turesson has found two separate types, which have been treated by Wilmott as subspecies of *F. vivipara*, viz. ssp. *killinensis* (from Killin in Perthshire) and ssp. *scotica* (widely distributed in Scotland).

than viviparous ones, but in certain high-mountainous areas, where the climatic and edaphic conditions are especially favourable for viviparous strains, such may locally supersede the seminiferous strains". The exclusively viviparous species may occupy a rather large area.

The viviparous form of *Poa alpina* in the British Isles is more frequent than the non-viviparous, which, as far as I know, has been recorded from four localities in Scotland (Lochnagar, Ben Lawers, Caenlochan and Glen Callater) and from one in Yorkshire (Ingleborough). It seems that the non-viviparous form of *P. alpina* was more widespread in the glacial period and has been now disappeared in many localities owing to the warmer climate. The viviparous forms probably may be more resistant to changes of climatic and edaphic conditions. As regards Scandinavia, non-viviparous *P. alpina* has a wide range there, being distributed everywhere in northern Scandinavia. It occurs also as a glacial relict in some parts of Central and S. Scandinavia, e.g. in some localities near Stockholm and Uppsala, on the islands of Öland and Gotland, where it grows on sunny cliffs. The viviparous forms of *P. alpina* on the contrary are frequent in the mountains of northern Scandinavia, but are absent in the southernmost mountains.

As mentioned by Turesson (1926-7, 1929-30, 1931) in *Festuca ovina* and by Nygren (1949) in *Deschampsia alpina,* the forms showing the greatest degree of vivipary are those which have a higher chromosome number. Nygren (1949), as also Lawrence (1945), has succeeded in obtaining a viviparous form of *Deschampsia caespitosa* in cultivation of a normal type by changing the growing conditions—the length of day. Only the northernmost biotype, from 68° N. latitude (from Abisko in Lapland) cultivated at 60° N. lat. (at Uppsala in Middle Sweden), being exposed to light for eight hours every day during two months, was affected as regards vivipary. The viviparous types of *Deschampsia alpina, Festuca vivipara, F. rubra* f. *vivipara, Poa × jemtlandica, P. × herjedalica* and *P. arctica* var. *stricta* in the same conditions preserved the vivipary even after the experiment. Nygren has arrived at the conclusion that the formation of bulbils in *Deschampsia* is due to variations in the length of daylight. His assumption is in agreement with Harder's (1948) investigations on *Kalanchoë Blossfeldiana* Poelln. According to Harder, the development of the flowers depends on special hormones, the formation of which are influenced by photoperiodism. Nygren writes (1949, p. 31): "Everything speaks in favour of different hormones and the moment of their action being genetically fixed and combined with a special life-rhythm. Disturbances of the normal rhythm—which may be of other kinds than in *Deschampsia*—will, depending on their degree, cause irregular meiosis, diplospory, apospory, or vivipary". These experiments are a valuable explanation of the origin of the viviparous and apomictic forms.

The viviparous hybrids, e.g. in the genus *Poa,* can be produced only in localities where one of the parents is represented by a viviparous form. It may be of interest to note, that the viviparous forms have usually well-developed pollen grains, but do not give seeds. The hybrids between a non-viviparous and a viviparous form are able to propagate themselves by bulbils, and therefore they are much commoner than the hybrids between non-viviparous species.

Polyploidy is widespread both in the British and Scandinavian mountain floras. Many authors, e.g. Tischler (1935), Löve & Löve (1943, 1949) and Flovik (1940), have studied the relation between polyploids and distribution. It has been found that frequency of polyploids increases with higher latitude, higher altitude or in extreme edaphic conditions. This phenomenon has been ascribed generally to the greater hardiness of polyploids, but this assumption has been criticized by several authors. Stebbins (p. 347) has pointed out ". . . no general rules can be formulated to govern the relation between the distribution of polyploids and diploids at least at present." Tropical and Southern Hemisphere plants are still little investigated from the cytogenetic point of view in comparison with those of the temperate and arctic floras. According to him, the higher percentage of polyploids in northern latitudes could be explained by the fact that the floras of these regions contain a high percentage of perennial herbs (hemicryptophytes) which are more favourably disposed toward polyploidy than woody plants and annuals. The origin of polyploids may have been promoted by very drastic changes in climatic and edaphic conditions, especially during the Ice Age. As shown by many authors (cf. Stebbins), the polyploids possess wide ranges of tolerance of environmental conditions, and they are peculiarly fitted to occupy new areas, e.g. resulting from glacial recession. Due to these causes the floras of montane and boreal regions are rich in polyploids.

The processes of mutation also play a considerable role in the changes of the mountain flora. The reasons for the origin of the mutants are still insufficiently investigated. It seems, however, that environmental factors, such as cold, heat, radiations and certain chemical substances in the soil could promote the changes in the hereditary material, associated sometimes with new characters in the plants. Many of the mountain species and peculiar biotypes have such origin. The best known mutants are polyploids, which have originated by doubling of the chromosome set in a non-hybrid plant. Thus *Arenaria norvegica* ($2n=80$) may have arisen from *A. ciliata* ($2n=40$), *Empetrum hermaphroditum* (Lange) Hagerup ($2n=52$) from *E. nigrum* L. ($2n=26$) and *Primula scotica* ($2n=54$)* from *P. farinosa* L. ($2n=18$).

*It is replaced by *P. scandinavica* Bruun ($2n=72$) in Scandinavia (Norway).

Floristic, cytogenetic and taxonomic investigations reveal that the British and Scandinavian mountain floras have a common ancient history, and the changes in the species composition in both floras are influenced by the similar climatic and edaphic factors combined with processes of evolution.

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THE NORTH AMERICAN AND LUSITANIAN ELEMENTS IN THE FLORA OF THE BRITISH ISLES

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The Lusitanian and North American elements have long been a central theme in discussions on the geography of the British flora. The plants of the former have engaged the attention of British botanists since the days of Forbes, now more than a century ago, and the interest of the latter has increased steadily as one by one its members have been added since the discovery of *Eriocaulon septangulare* and *Spiranthes Romanzoffiana* in Ireland during the early years of last century to the recent additions of *Myriophyllum alterniflorum* var. *americanum* and *Potamogeton epihydrus*.

I suppose that most botanists who have discussed these groups in the last century—and the list is a long and distinguished one —would have contended that an understanding of their present distributions would contribute materially to elucidating the history and origin of the British flora as a whole. But it is becoming increasingly clear that a certain danger lies in isolating these —or for that matter, any—particular "elements" in the flora for special consideration. They are so isolated because they are considered exceptional, and it no longer seems so obvious in dealing with problems of historical phytogeography that elements with exceptional distributions necessarily hold the key. Exclusive concentration on bizarre types of distribution may retard progress towards the understanding of the origins of our flora by over-simplifying the problems involved, while simultaneously concealing the evidence with which they may be solved. Species with such distributions must be examined first in relation to the other components of the flora, which is how the Lusitanian species were viewed some years ago by Stapf (1913, 1916) and later by Matthews (1926, 1937), and how more recently some of the species forming the so-called North American element have been treated by Hultén in his studies of distributional problems in the boreal and arctic floras as a whole.

The difficulty of finding a universally acceptable definition of these two elements, the North American and Lusitanian, testifies to the artificiality of the concepts involved. There is agreement on what might be called the extreme examples of the types of distribution associated with the names, but where the line is to be drawn as species with greater and greater continuity of area are taken into account seems largely a matter of personal taste. Is *Naias flexilis,* with a fairly extensive extra-British European range, to be counted a member of the "North American" element

in our flora? If so, why not *Lobelia Dortmanna*? Similar questions could be posed in relation to the "Lusitanian" group. However, some basis of discussion is desirable, and such is provided by the lists of the Lusitanian and North American elements supplied by that leading student of Irish phytogeography, Dr. R. Ll. Praeger. In Table I are the "Plants of Pyrenean-Mediterranean Facies" as listed in *The Botanist in Ireland* of 1934: the list is identical with that of the "Southern Group" in the Irish flora given in his address to the Royal Irish Academy in 1932, except for the addition of *Sibthorpia europaea, Pinguicula lusitanica* and *Euphorbia Peplis*. I have brought it up to date by making the nomenclatural changes necessitated by recent taxonomic work. Table II comprises the "Plants of North American Facies" of *The Botanist in Ireland* (the "American Group" of 1932). Here again I have brought the list up to date and have added the recent finds of North American species which undoubtedly would have been included in this group by Praeger, *Myriophyllum alterniflorum* var. *americanum* and *Potamogeton epihydrus* var. *Nuttalli*. The former, the only form of *Myriophyllum alterniflorum* present in Lough Neagh, was identified with that widespread in North America by Pugsley in 1938, and the latter has now been found in Scottish stations where it seems beyond suspicion of human introduction. Its distribution is discussed by J. W. Heslop Harrison (1949, 1950, 1952) and Taylor (1949).

TABLE I

"Plants of Pyrenean-Mediterranean Facies"
(Adapted from Praeger, 1934)

	Ireland	*Britain*
Saxifraga spathularis	S., E., W. & N.W.	—
S. hirsuta	S.W. & W.	—
Arbutus Unedo	S.W. & W.	—
Erica mediterranea	W.	—
E. Mackaiana	W.	—
E. ciliaris	—	S.W.
E. vagans	—	S.W.
Daboecia cantabrica	W.	—
Sibthorpia europaea	S.W.	S.W. & S.
Pinguicula grandiflora	S.W.	—
P. lusitanica	Gen.	S.W. & W. Scot.
Euphorbia hyberna	S., W. & N.W.	S.W.
E. Peplis	S.	S.W. & S.
Neotinea intacta	W.	—
Simethis planifolia	S.W.	—

TABLE II
"Plants of North American Facies"
(After Praeger, 1934, with additions)

	Ireland	*Britain*
Spiranthes Romanzoffiana (incl. *S. stricta* & *S. gemmipara*)	N.E. & S.W.	Coll, Colonsay W. Argyllshire
Sisyrinchium angustifolium	S.W.-N.W.	(introd.)
Juncus tenuis	S.W. (also introd.)	(introd.)
(*J. Dudleyi*	—	Scotland, probably introd.)
Naias flexilis	S.W.-N.W.	N. & W.
Eriocaulon septangulare	S.W.-N.W.	Coll, Skye
Potamogeton epihydrus var. *Nuttallii*	—	South Uist
Myriophyllum alterniflorum var. *americanum*	Loughs Neagh, Ree & Derg	Tiree

Praeger lists a dozen or so invertebrate animals whose distributions he associates with those of the Lusitanian plants, and the fresh-water sponge, *Heteromeyenia ryderi,* which he places with the North American group; I shall not have occasion to discuss these in detail, but of course their presence in the western parts of the British Isles is relevant to the corresponding plant groups. Equivalent "elements" can be defined among non-vascular plants also (see for example Watson, 1935, and Greig-Smith, 1950).

The status of these plants of the Lusitanian and North American groups in the flora is evidently a matter of some importance, for clearly if they are recent human introductions they cease to have any phytogeographical significance whatever. Of the Lusitanian species, most authorities are prepared to accept that they are native in all of their Irish stations. The northernmost outpost of *Arbutus Unedo,* around Lough Gill in Co. Sligo, originally considered an introduction, is now looked upon as natural (Praeger, 1932; Sealy, 1949). Another station for *Pinguicula grandiflora* has recently been detected in Co. Clare, so that it seems likely that it is truly native in that county. Outside of Ireland, some of the Lusitanian species of Praeger's list are not so well authenticated. *Pinguicula grandiflora* is known to have been introduced in Cornwall; *Simethis planifolia,* accepted as native in Dorset by Stapf, Praeger and others has recently been considered as more likely introduced (Good, 1948), and *Sibthorpia europaea,* recorded from the Outer Hebrides, is undoubtedly an introduction there. Of the North American species, a higher percentage has at least some doubtful stations. *Juncus tenuis* is considered by Praeger as native in Kerry; it is said to occupy some natural-looking habitats there, although it is also a common plant of road verges in the same area. Elsewhere in Ireland, as for example

near Belfast, it is undoubtedly a recent arrival, as also probably in Great Britain and on the Continent. *Juncus Dudleyi* should probably be deleted from the list, for almost certainly it is a recent introduction in its one or two Scottish localities. The status of *Naias flexilis* has been impugned in some of its Britannic stations; nevertheless, most authorities seem prepared to accept it as native in the areas listed in Table II. *Sisyrinchium angustifolium,* generally regarded as native in its western Irish stations, is naturalised in several localities in Great Britain and on the Continent. It also has stations in the Carpathians at rather high altitudes where it has been considered native.

Neither in the case of *Sisyrinchium angustifolium* nor *Juncus tenuis* is it known as yet whether or not the form which has run wild in Europe is identical with that occupying natural habitats in the west of Ireland. Apart from these two species, of the history of the plants composing the classical Lusitanian and North American elements during the period of human observation one thing can be asserted with some assurance, that none has shown anything like the spectacular tendency to spread outwards from the original stations that has been characteristic of so many aliens introduced within the same period. It is true that new stations have been recorded from time to time for nearly all of them, but this has been largely the result of the spread of botanists rather than of the plants. Time does not allow a consideration of the evidence for each species, but it may be noted that for *Arbutus Unedo* there is even some evidence of fairly recent reduction of area (Praeger, 1932). The various Lusitanian heaths are apparently capable of regenerating actively enough within the areas they occupy, but those areas are remarkably restricted, and notwithstanding the assertion of Clement Reid (1911) that they are spreading vigorously, none seem to have extended their ranges appreciably during the long period of human observation.

Let us now turn to the phytogeographical problems supposedly associated with these groups. It is fairly obvious in the first place why they have attracted such attention during the last century. The circumstances of their occurrence in the British Isles—fairly common in restricted areas of the extreme west or south-west, but absent from much of the country—has contributed almost as much as the fact of the geographical remoteness of the main centres of distribution of the species concerned to hold the attention of botanists. Interest in the species for these reasons has led to speculation as to their history, and in particular as to their time and mode of arrival in their present stations. Divergence of opinion relating to the latter points has led to protracted (often almost passionate!) controversy, which has involved biologists, geologists, archaeologists, ethnologists and climatologists—in fact, practically all interested in the quaternary history of western Europe. The main controversy has, of course, revolved around a familiar issue of which we have already heard something during this conference: whether or not any portion

of the biota of the British Isles survived all or any phases of the Pleistocene glaciations. In relation to this issue, the so-called Lusitanian and North American elements have been occasionally associated with the arctic-alpines as of similar relevance, an association which we now see to have been somewhat unfortunate.

Broadly speaking, those who have written or spoken on the subject have fallen into two groups: those convinced that we have to go back as far as pre-glacial (or at least inter-glacial) times to find an explanation for the present areas of these species, and those who consider the Britannic part of the present areas to be of relatively recent, post-glacial, origin. Forbes may be considered the pioneer of the former school; in his distinguished footsteps have followed Scharff, Praeger, Wilmott and many others, and there has been a weighty contribution to the arguments advanced by these workers, both directly and by analogy, from foreign students of similar problems, amongst whom one may mention Du Rietz and Fernald. Those convinced of the glacial extermination of the major portion of the British biota (and thus of the opinion that present areas are post-glacial in origin) have included Geikie, Engler, Clement Reid, Stapf, Matthews, Charlesworth, Salisbury, and, more recently, Deevey.

It is an interesting enough pastime to fight old battles over again, but I think we may well on this occasion skip many of the details of former arguments and abstract only those points which to-day still seem to have relevance.

One purely botanical matter stands but little in advance of where it did quarter of a century ago: our knowledge of the rôle of seed dispersal in plant distribution. Dr. Praeger's tests of 1913 remain the latest of an experimental nature concerned with the plants we are discussing. As is well known, their results led him to dispute Clement Reid's assumption of long range chance dispersal as an important factor in explaining, *inter alia,* the present ranges of the Lusitanian species. Most botanists, including ecologists and plant geographers best equipped to judge, seem convinced that rapid seed dispersal over great distances is not a major factor in plant distribution. Particularly where advance into territory already occupied by closed communities is involved, extension of area seems to be attained by continuous intensive short-range dispersal. This presumption underlies the time-and-distance relationship basic to Willis's theory of age-and-area, as well as to the more recent theory of equiformal progressive areas so brilliantly developed by Hultén (1937). Nevertheless, we cannot entirely exclude the possibility of long-range random dispersal followed by ecesis, *particularly where open communities are available for colonisation, or where ecological niches are available to be filled.* Dr. Godwin has pointed out how favourable for the rapid spread of many opportunist species, now regarded as weeds of cultivation or ruderals, were the open habitats of late-glacial times, exposed by the retreating or decaying ice. Nearer to our own times we may point to the rapid spread to remote "native"

localities of various aliens which have found favourable ecological niches in Britain, for example *Elodea canadensis* and *Epilobium pedunculare,* and in the case of native species, the remarkable speed with which local and often "rare" plants like *Ophrys apifera* are able to colonise calcareous waste-heaps, often in huge numbers. It may be of considerable phytogeographical significance that the course of recolonisation of such habitats as these bears little relationship to that to be expected from the orthodox postulates of ecological succession. The *first* colonists of completely unhumified soils in clay-pits, limestone quarries, and the like are frequently shrubby or arboreal species, and in the early stages, while the community is still open, very strange mixtures indeed of calcicole and calcifuge species appear in such habitats.

The importance to historical plant geography of these considerations relating to dispersal can hardly be over-emphasised. If rapid long range establishment takes place to any large extent, or if it did take place when communities were less crowded than now, then the modern ranges of species present mainly problems of *ecology* and cease to have much value in the interpretation of *history*. That species rarely occupy all of their potential areas, and that their ranges are so often limited by physiographical barriers, provides good evidence that dispersal is often—perhaps generally—inadequate for rapid colonisation at great distances from points of origin. But it is impossible to assert categorically that such has *never* taken place, and in any specific case it may be that the path of discretion lies in accepting the possibility rather than insisting on moving a continent or sinking a land bridge to explain a particularly troublesome area.

Among native British plants the North American species listed in Table II have probably the greatest discontinuities in their areas. An indication of the distributions of some of the species which form the classical North American element is given in Fig. 10. It will be seen that all of the species overlap in eastern North America, and although there are various points of dissimilarity in the remainder of their American ranges, there is clearly every reason for grouping them together in discussing their distribution on the two sides of the Atlantic. Of course, these are by no means the only species with an "amphi-Atlantic" distribution, for a fair proportion of British plants has natural ranges in North America. Many are species of a rather "northern" character. Considering the flora of the hemisphere as a whole, it is true to say that while many arctic and sub-arctic species have complete or almost complete circumpolar ranges, the degree of community between the Old and New World floras decreases progressively southwards—a fact illustrated by the absence of any arboreal species common to Europe and North America except *Juniperus communis.* What attracts special attention to the group we are at present considering is that they are boreal species which possess markedly asymmetrical ranges on the two sides of the Atlantic. Dr. Praeger has tentatively added to their number as offer-

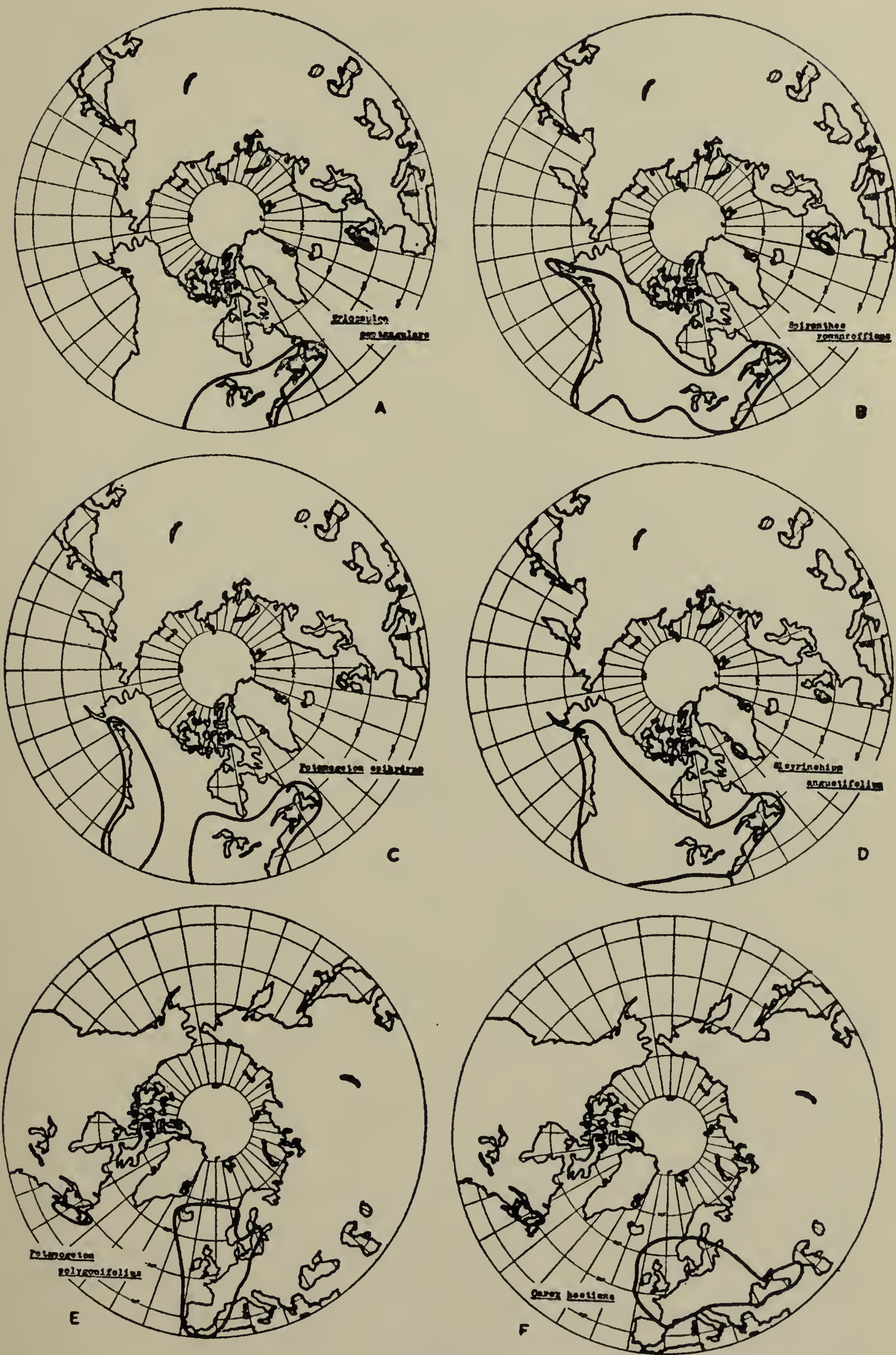

Fig. 10.

ing a similar problem certain Scandinavian species such as *Campanula uniflora, Pedicularis flammea* and *Rhododendron lapponicum* (1939). These species are arctic or arctic-montane; their affinities lie with arctic and sub-arctic circumpolar species, and it does not seem likely therefore that their asymmetry of area has necessarily arisen in the same manner as that of the Britannic-North American species. However, an analogous problem does appear to be presented by the group of species the areas of which form, as it were, mirror images of those of Table II, with main centres of distribution in Europe and minor additional areas in North America. Figures 10e and 10f illustrate the ranges of two of these—*Potamogeton polygonifolius* and *Carex Hostiana.*

To explain these occurrences of common European plants in such restricted areas in eastern North America, similar suggestions have been made to those put forward for our own North American species. Phytogeographers in both Europe and America have been reluctant to accept the possibility of direct dispersal across the intervening seas, and have been practically unanimous in the contention that these present areas are "relict" ones, representing the remains of once continuous distributions. The nature of these continuous distributions has been variously conceived. Irish biologists have mainly thought in terms of complete or partial Tertiary land connections, presumably along the line of the Wyville-Thompson Ridge, across which these and other amphi-Atlantic species could have migrated. Hultén (1937) has strongly urged the view that continuity was in the other direction, and that the former areas of these species lay through Siberia and Alaska during the great interglacial.

Whichever view of the original continuous area has been accepted, the subsequent disruption which has led to the present patterns has been put down to glaciation, the ice or the associated glacial climate having eliminated these plants throughout much of their ranges. Similar vicissitudes must, of course, have been experienced by all other boreal species, including the many more symmetrical amphi-Atlantic species whose present distributions have led to no special phytogeographical comment. The essential difference between these and the "asymmetrical" species seems to be that while it is quite acceptable that the former survived the glacial periods well south of the ice-sheet in each continent and spread north subsequently to occupy their present fairly extensive ranges in each, it is extremely difficult to say why, if the asymmetrically distributed species had a similar history, they have now no representatives outside of the formerly glaciated area on the side of the Atlantic on which they possess their minor areas. Whereas it can be argued in the case of the amphi-Atlantic arctic and sub-arctic species that they have migrated northwards into their present stations within the glaciated area and have become extinct in their southern refuges because of amelioration of climate or pressure of competition there, there seems no such ecological reason why plants like

Spiranthes Romanzoffiana and *Eriocaulon septangulare,* which have coastal and inland ranges in North America at low latitudes, should not have persisted in France or England or elsewhere along the path of their northward migration in Europe if indeed they existed through the glacial period in a refuge *south* of the periglacial zone. This is the heart of the problem which these species present, and it may be noted in passing that Deevey's (1949) facile disposition of it is no more than a restatement of part of it in other terms.

Both Praeger's and Hultén's views on the history of species such as *Spiranthes Romanzoffiana* involve implicitly or explicitly the suggestion that they survived one or more glacial periods in or near their present localities in Europe, possibly on low-lying ice-free coastal land, now submerged. Similar views have been put forward by North American botanists for the equivalent group on the other side of the Atlantic. Hultén quotes *Dulichium spathaceum* as an example of a species lost to Europe during Pleistocene times because it failed so to survive, and Marie Victorin mentions *Trapa natans* as an equivalent American loss.

It must be admitted that the evidence presented by Hultén in the form of corresponding ("equiformal") but less dissected areas is extremely weighty, but there are certain other facts about the species with extreme restriction of range in western Europe which are relevant here. Thus their behaviour in Ireland and the Hebrides shows certain unusual features. *Spiranthes Romanzoffiana* may be taken as an example: according to Praeger, it is an active colonist of cut-away bog as around Lough Neagh, and that despite the fact that there are few years when it sets seed in Northern Ireland. But its area remains small, and furthermore, the range of habitats which it exploits in Ireland and Scotland is very narrow compared with that which the same species occupies in North America, according to Correll. One may well deduce from this that we possess what Hultén would call a biotype impoverished race, capable of exploiting vigorously one narrow range of habitat-type (in this case lake-margin bog and peaty pasture) but limited by the availability of that habitat-type. Much the same may be said in the case of *Eriocaulon septangulare* in Ireland and the Hebrides. In parts of western Ireland it apparently possesses an extraordinary capacity for colonisation, occupying even small peat pools in the middle of miles of blanket bog. What then has prevented it spreading further afield in the long period it has had in that country, since we know from the work of Jessen (1949) that it was present there in the early part of the Atlantic period (Zone VIIa)?

The narrow ecological amplitudes of the species of the Britannic-American group would accord well with such a history as the "survivalists" have proposed for them, since genetical impoverishment would, one may imagine, be a likely result of a long period of confinement in a small marginal refuge in a period of rigorous climate. But a race of a species which is of low genetical varia-

bility may have arisen in another way than through biotype elimination *in situ* from one of high variability formerly occurring in the same area. A population which has arisen entirely from *one or two introductions of seed* would also be of low genetical variability if insufficient time has elapsed since introduction for variability to be enriched by mutation.

Before considering the implications of this, let us look once more at the classical North American plants as a group. An outstanding feature is that they are all aquatic, marsh or lake-margin plants, at least in their Britannic areas. *Spiranthes Romanzoffiana* is, of course, terrestrial but its area in north Ireland is strikingly associated with Lough Neagh, and its other stations in the south of Ireland and on Coll and Colonsay are also in the neighbourhood of lakes. The North American sponge, *Heteromeyenia ryderi,* often associated with the plant species, similarly frequents fresh-water. The ecological distribution of all of these organisms is such that their propagules might quite conceivably be all transportable by the same agency.

Dr. Praeger stated in 1932 that he was not aware of any bird which regularly crossed the North Atlantic; but subsequent studies of bird migration have shown that some do, and large ones at that. Mr. Sullivan, an Irish lighthouse-keeper, has very recently (1950) drawn attention to one in particular in connection with the problem we are discussing—the Greenland White-fronted Goose, *Anser albifrons flavicornis.* This race has only recently been recognised by Dalgety and Scott, and it has now proved to have an unusual migrational tract which is illustrated in Fig. 11.

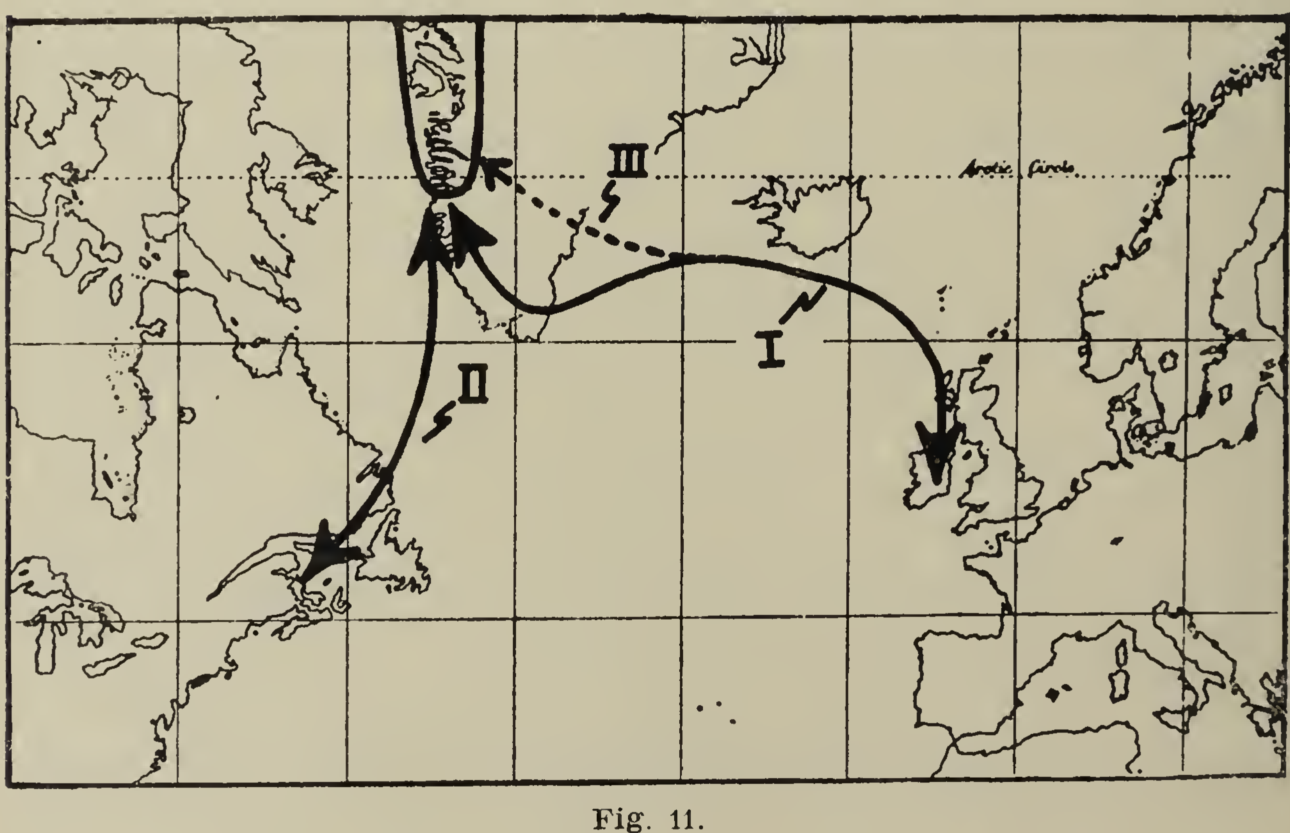

Fig. 11.

Some North Atlantic goose migration routes. I. Route of Greenland White-fronted Goose. II. Route of certain North American migrants, and occasionally of Greenland White-fronted. III. Occasional route of Greenland White-fronted.

According to the data of Salomonsen (1950) the main breeding area of this bird is in north-western Greenland, inland almost to the edge of the ice-cap, from Sukkertoppen to Christianshaab, where enormous numbers congregate around lake margins throughout the summer. The interesting point is that a large proportion of the Greenland flock winters in Ireland, a few birds occasionally visiting north and west Scotland (including the Hebrides) and north Wales. The departure from Greenland is in September, and the flock takes well under a month to reach Ireland. The return journey is made in late April and May. In addition to this migration route, it appears that some part of the flock at least may winter in North America in the region of the mouth of the St Lawrence, while various other goose species, while not visiting Europe, breed in the same parts of Greenland and regularly winter in eastern Canada.

The Greenland White-fronted Goose is a bird of fair size, feeding largely on water-weeds and spending a good deal of its time wading about through lake-side mud. Very large numbers make the annual trans-North Atlantic migration, and probably have been doing so since early post-glacial times. It is difficult to make any sort of accurate estimate, but in that period some scores of millions of bird-journeys may have been made across the Atlantic. Personally I feel it would be quite incredible that never once in all these journeys should a single viable seed have been transported from a lake-margin on one side of the Atlantic to a lake-margin on the other. Transport of common species already occurring on both sides of the Atlantic would of course be of no importance: transport of odd seeds of species not already present would result in exactly what we have—local colonies consisting of one or a few biotypes growing well enough in habitats similar to those from which they came, but without capacity for much expansion outside of them.

It is true that the crossing envisaged is not a direct one, being via Greenland, which may be north of the present-day potential permanent range of some of the species concerned. But permanent establishment in Greenland would not be essential to allow a crossing in two stages. The status of many of the water plants known to occur in western Greenland is very curious. According to Porsild and others who have studied the aquatic vegetation, the various species of *Potamogeton, Utricularia* and the like occur locally and fluctuate greatly in number from season to season. While they may have been more firmly established there during the post-glacial climatic optimum, many fail to produce seed nowadays and are probably dependent upon constant reinforcement from more southern latitudes, almost certainly through the agency of water-fowl. The same is probably true of lake-margin plants, and it cannot be without significance that the most northerly station for *Sisyrinchium angustifolium* is in north-western Greenland, within the breeding area of the Greenland White-fronted Goose.

Let us now turn to the Lusitanian species. These occupy a greater range of habitats, although there is certainly a preponderance of moorland and heath plants among them. Again they are mostly quite abundant in the areas where they do occur, but as I have already emphasised, it is a striking fact that none of them is showing positive signs of active spread. Clement Reid's assertion that such was the case has been refuted by Praeger and others with life-long knowledge of the plants in the field.

We have positive evidence for only a few, but there seems little reason to doubt that these species are not nowadays spreading because they are climatically limited to their present western fringing areas. It is common knowledge that different climatic factors are often found to be limiting at different boundaries of a species area, and frequently the limit is imposed by subtle combinations of factors which may not be apparent from any isolated climatological datum. It might therefore be misleading to select any particular one for special emphasis, but it seems very probable from Sealy's careful analysis of the tolerance of *Arbutus Unedo* that in the case of this species the northward limiting factor along the Atlantic seaboard is winter cold, even although elsewhere in regions of warmer summers it may be capable of tolerating more extreme winter temperatures. Other checks to range-extension, operative during the summer, may be at work in the case of other Lusitanian species, for I understand from Dr. Webb that *Euphorbia hyberna* fails to produce seed in cultivation even as near to its native areas as Dublin.

Nevertheless, taking the group as a whole and neglecting for the moment the matter of area discontinuity, we see that the northward extension up the Atlantic seaboard could be regarded simply as a corollary of the special climatic conditions prevailing there, best revealed by the well-known trend of winter isotherms. Exactly similar northward extensions occur in the Scandinavian flora. *Erica mediterranea* and *E. Mackaiana* in western Ireland can be matched in western Norway by *E. cinerea* and *E. Tetralix,* and the Lusitanian saxifrages by species like *Primula vulgaris* and *Chrysosplenium oppositifolium.* The implications are inescapable: if this western fringing distribution is imposed by climate, then a very slight deterioration indeed would suffice to eliminate the area completely within which these species can survive.

This seems to bode ill for the thesis of per-glacial survival in or near the present localities. Sealy (1949) has suggested that the 40° mean January isotherm may be a climatic limit for regeneration of *Arbutus Unedo* in north-western Europe. The most recent estimates for Pleistocene climates are those of Professor Manley (1951); in drawing these up he had the botanical problems in mind. He offers the following:

		Older Drift glaciation	Newer Drift glaciation	Scottish readvance (Zone I)	Allerød (Zone II)	Perth readvance (Zone III)	To-day
Outer	July	40	40	42	46	44	56°F.
Hebrides	Jan.	23	23	25	25	25	42°F.
South	July	46	46	48	53	49	61°F.
Cornwall	Jan.	24	24	28	31±	31±	45°F.

Most favourable possible conditions at the glacial maximum in Kerry, July: 48°F., January: 31°F. (a little cooler than western Tierra del Fuego to-day).

Recent estimates by Klute (1951) are even less favourable.

If these figures are at all representative of the actual conditions during the glacial maxima, they evidently rule out decisively the possibility of survival of any species with a January mean limit of 40°F. like *Arbutus Unedo*. Over the long period involved, it is difficult to imagine any compensatory factor short of hot springs which could produce a microclimate so very much more favourable than the prevailing regional climate during the glacial advances as that which would be required for even local persistence of species requiring practically frost-free winters, at least when growing in our latitudes.

Fig. 12. Distribution of *Rubia peregrina.*

Professor Jessen's investigations of Irish late-glacial deposits have led him to similar conclusions: at any rate for *Arbutus Unedo* he considers *in situ* survival of even late-glacial climates highly improbable.

If per-glacial survival in the Britannic area is ruled out—and the weight of evidence seems now strongly against such a hypothesis—post-glacial immigration of the Lusitanian species must be presumed. Here again we are faced with the difficulty of explaining the present considerable discontinuity of area, and the absence of some of the Irish-Lusitanian species from Britain. However, the matter of area discontinuity must be viewed in its correct perspective. One of the most successful attempts to do this was that of Stapf (1916), in which an avowed aim was to analyse the areal inter-relationships not only of the "classical" Lusitanian group we are now considering, but of other southern species with cognate patterns of distribution.

Stapf compiled a list of 142 British vascular species with a "southern" type of distribution, not including plants of arable land. Of these, 95 were non-littoral. Dividing the species according to whether or not they extend into the Eastern Mediterranean region, he recognised two distributional types in the southern element: the Atlantic and the Mediterranean. Examples of species with a "Mediterranean" distribution are *Rubia peregrina* (fig. 12) showing continuity up the Atlantic seaboard into Britain, and *Arbutus Unedo* (fig. 13) with an area almost coincident in the

Fig. 13. Distribution of *Arbutus Unedo*.

Mediterranean but more dissected in the north-west. Two "Atlantic" species may be taken to show similar contrast in continuity—*Erica ciliaris and Daboecia cantabrica* (fig. 14).

The juxtaposition of these maps illustrates Stapf's point of view regarding the so-called Lusitanian species: to him they represented no isolated problem, but simply "cases of far gone disintegration of area" in a sequence which could be built up towards complete continuity. Stapf, like Hultén, was thus an exponent of the idea of equiformal progressive areas.

If it is accepted that the present areas are the remains of former continuous ones and not the product of recent long range dispersal, then it is logical to seek a period when conditions were such that the Lusitanian and other southern species in the British flora are likely to have possessed more extensive northerly ranges than at present. Obviously such a period would be during the post-glacial climatic optimum, knowledge of which has been gained in north-western Europe through study of fossil records of just such phenomena as we are seeking to establish—northward or upward extension of the ranges of organisms now climatically limited to lower latitudes or altitudes. Evidence from marine molluscs suggests a sea temperature around Britain during the

Fig. 14. Distribution of *Erica ciliaris* L. and *Daboecia cantabrica* L.

optimum some 3° F. higher than to-day. By an elegant application of the holly, ivy and mistletoe as climatic indicators, Iversen (1944) has arrived at estimates for central Denmark for the Atlantic period of *c.* 3·5° F. above present day mean for July, and *c.* 1° F. above present day mean for January. There is, of course, a danger in transferring these estimates to the oceanic parts of the British Isles. Nevertheless, it seems likely that while the excess of summer means over those of the present day in our area may have been relatively lower than in central Denmark, the sustained winter means were relatively higher. There can be little doubt that were the Lusitanian species present then, they, like other thermophile species, are likely to have possessed more extensive ranges in the Britannic area than at present. The subsequent climatic deterioration and competition from hardier plants would be adequate to explain the present severe restriction of area, evidently still progressing, as can be seen from the example of Mediterranean plants like *Otanthus maritima* and *Euphorbia Peplis,* the ranges of which are shrinking and becoming more fragmented almost before our eyes.

At least one of the classical Lusitanian group—*Erica Mackaiana*—is known to have been in Ireland near its present stations in late Boreal and early Atlantic times (Jessen, 1949), and the conditions then were probably favourable for the existence of all. We have as yet no direct evidence as to how much earlier than this they arrived, nor as to what route their migration followed.

Evidently the answers to these problems are closely connected with three other issues—(a) the rate at which these species are capable of invading new territory in which conditions favourable for their growth prevail; (b) the rate at which such conditions were established in the Britannic area after the inimical climate of late-glacial had passed away, and (c) the availability of land surfaces for their migration during the period of climatic amelioration.

There is little direct evidence relating to the first of these issues. Estimates of the movement of climax forest formations in North America obtained from application of the radio-carbon dating technique suggest that migration of a whole community can average out at something like half-a-mile a year, and pollen studies have shown that spread of species like beech and spruce in Europe may have been slower than this. However, these examples of movement of forest trees probably have little or no application here. Where suitable open habitats are available, the limiting factor in the expansion of area may be the capacity of a species to obtain rapid and abundant seed dispersal over moderate distances. Small-seeded species with large seed-outputs may have a considerable advantage in such circumstances, notwithstanding their lower capacity for establishment in closed communities where the advantage probably lies with possession of large seed food reserves.

As for the question of the rate of establishment in post-glacial times of favourable climatic conditions for the spread of southern species along the western European seaboard, it seems that any view that presumes something of the nature of a "wave" of climatic improvement advancing northward would be wide of the truth. Rather must we think of the amelioration as a regional effect, involving the maintenance over a period of years of higher average temperatures. If the present trend of winter isotherms prevailed, it may well be that a coastal strip of considerable length became very quickly available for colonisation by plants and animals previously confined to their Lusitanian refuges. As suggested above, in such conditions dispersal capacity alone may have controlled the rate of immigration of species. The rate of spread of *Arbutus Unedo*, with its vast seed output, may at one time have been as spectacular as that of *Buddleja Davidii* on London bombed-sites.

In seeking to establish the probable migration route, we are met with the vexed question of early post-glacial sea levels. Dr. Farrington has recently (1945) arrived at an estimate for sea-level depression off southern Ireland of *c.* 400 ft. at the beginning of the post-glacial period. A depression of this order would eliminate the English and Bristol Channels and provide a broad strip of dry land south of the present Wexford coast. St. George's Channel would not entirely disappear (presuming the present submarine contours prevailed then), but dry land in Cardigan Bay would be separated by but a narrow water barrier from similar low-lying land off the Wicklow coast.

How long into post-glacial times these conditions persisted is problematical, but it is known from Dr. Godwin's work on the moor-log from the Dogger Bank in the North Sea that peat formation there persisted actively until perhaps the middle of the Boreal period, when the cycle of climatic amelioration was well advanced.

Clearly the northward movement of organisms from the Lusitanian survival centres could have been conditioned by two processes occurring simultaneously: the climatic amelioration encouraging the northward spread, and the gradual submergence of the coast-line and fragmentation of the land-route over which that spread was possible.

If we view the southern group (as defined by Stapf) as a whole, it is then to be regarded as being composed of those species which exploited rapidly the new climatic conditions along the western European seaboard, and made the precarious journey northward along the disintegrating coast-line before the gaps in the overland route became too great for normal dispersal processes effectively to span. The gradient from the oceanic coastal climate to the inland continental one may have been steeper than it is to-day, and the belt along which establishment was possible may well have been a narrow one.

The present marked discontinuities of range which many of the species show is then to be attributed partly to submergence of former land surface, partly to area shrinkage in later periods of climatic deterioration, and partly to extermination through the appropriation of their habitats by hardier or better adapted species. The cases of "far gone disintegration of area" form the classical Lusitanian element, species which have been selected for special consideration simply *because* of this fact and having little else in common except their present climatic limitation in our area.

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It was not possible to allow time for discussion after this paper. The following contribution by Dr. H. G. Baker was handed in at the Conference and it is printed here with the agreement of Dr. Heslop-Harrison : —

Dr. Heslop-Harrison's paper represents a very valuable contribution. His demonstration that 'long-distance' dispersal cannot be ruled out in considering the advent of the 'American' element in the British flora is worthy of serious study from all points of view.

Limonium humile Mill. is not generally included in this element of the British flora although it occupies a place in the 'Oceanic Northern' element of Matthew's classification where the 'American' element is also to be found. In fact, all the links of this species are with America. Apart from its occurrences in the British Isles, it occurs only at Brest and in stations at the mouth of the Baltic. In morphology it agrees very closely with the species of the same subsection of the genus which are found along the Atlantic coast of North America and is also closely related to *L. Lefroyi* in Bermuda. Like the American species it is a tetraploid and self-incompatible (with the same combination of pollen- and stigma-morphology) and is the only European species of this subsection which is not dimorphic in pollen and stigmata (and, therefore, self-incompatible).

There is good evidence that dimorphic forms of *Limonium* emigrated from the Old World to South America, and the South American species form a morphological link with those of North America, although the latter are secondarily monomorphic. Thus *L. humile* is probably the most recent species in a long series and must have been derived from a re-crossing of the Atlantic from eastern North America to Europe. It agrees with Dr. Heslop-Harrison's postulates in being an inhabitant of a relatively open zone in the salt-marsh community, its fruiting calyces are quite likely to adhere to the feathers of birds and its self-compatible nature means that a seed-reproducing population may be started by the chance arrival of a single disseminule.

THE CONTINENTAL ELEMENT IN OUR FLORA

S. M. WALTERS.

In the eyes of any visiting Central European botanist, our flora is quite markedly 'oceanic'. Thus, even in what we are pleased to call our climatically 'Continental' areas in East Anglia, the heather, *Calluna vulgaris,* can dominate large areas of heathland; and *Erica cinerea* and *E. Tetralix,* which are typical oceanic plants of the Atlantic seaboard of Europe, occur throughout the British Isles. It is not, therefore, surprising to find that some of our commonest and best-known plants, such as the Primrose (*Primula vulgaris*), are absent from most of continental Europe including Scandinavia; although, of course, a large number of our species (Matthews (1937) calculated over half) are widespread in Europe or beyond. There are, however, a considerable number of species in our flora, usually rare or local ones, which are not common in W. Europe, but are common in Central and E. Europe; and it is these so-called 'Continental' species that I propose to consider.

Climate, it is generally assumed, is the factor controlling the broad outline of the distribution of species; and I assume that the main features of an oceanic climate are familiar to all of us. Our vegetation, like ourselves, is adapted to a mild, cool, damp climate with no great extremes of temperature throughout the year—a type of climate which operates, thanks to the Gulf Stream, up the Atlantic seaboard of Europe. In contrast, the continental climate of the main land mass of Eurasia offers much greater extremes, with hot, dry summers and hard, cold winters. We assume, therefore, that species common in continental Europe are adapted to the harsher climate, whilst many of our plants could not tolerate it.

Let us look now at the actual types of continental distribution represented in our flora. It is important here to look at the *total* range of the species; for although it is often true that a plant with, for example, a S. or S.W. distribution in Britain possesses a general European distribution of an Atlantic type, this is by no means necessarily the case, as we shall see in *Linosyris vulgaris* (an 'Atlantic' species in Watson's classification of British distribution types). In our Continental species we can, for convenience, distinguish three types, which I will briefly exemplify:—

1. *Continental Northern* (incl. Matthews' Northern Montane). This group includes characteristic species of the Northern coniferous forest (and, of course, *Pinus sylvestris* itself) such as *Moneses uniflora, Linnaea borealis, Goodyera repens,* etc., now rare or local in Britain, but presumably widespread when the Boreal coniferous forest covered much of the British Isles. This

Boreal element, which presents special features, will not be further discussed. The group, however, also includes a small number of species not tolerant of forest conditions which have, ecologically, affinities with the main continental element; for example the famous Teesdale rarities *Potentilla fruticosa* and *Viola rupestris,* and *Astragalus danicus* (to be mentioned later).

2. *Continental proper.* These species are widespread in C. Europe and many go over into E. Europe and Asia, where some at least are characteristic plants of the steppe regions, e.g. of European Russia. Matthews lists 82 species in this group. Perhaps the most-quoted example is *Veronica spicata.*

3. *Continental Southern.* This group, which grades into what could be called 'sub-Mediterranean' species, is larger (Matthews gives 127 species); it contains many interesting British plants, such as *Carex humilis,* a typical hill-steppe species of south Central Europe, with a scattered distribution across Asia. The Box-tree, *Buxus sempervirens,* has another similar distribution.

What are the main features of the distribution of such species in W. Europe, including the British Isles? As we might expect, they tend to show increasingly patchy and discontinuous areas as one goes west in Europe (or north and west in the case of many Continental and Continental Southern species). Such a distribution cannot, of course, be recognised by a mere outline range map; but if dot maps are prepared it becomes obvious. Discontinuities are in many cases very considerable; thus for *Dianthus gratianopolitanus,* the Cheddar Pink, its nearest Continental station, in the Belgian Ardennes, is over 400 miles away.

How far can we correlate the distribution of continental species with environmental factors? Clearly, so far as climate is concerned, there is, as we have seen, an obvious general correlation; and in fact the greatest number of different continental species in the British Isles are to be found in S.E. England, particularly the Breckland of East Anglia (where, of course, the soil factors are also highly peculiar). It is, however, important to notice that it is those species obviously dependent largely or wholly on seed production for their survival (e.g. annuals and Orchids) which show an impressive restriction of range to the climatically most continental areas of Britain (e.g. annual Veronicas of the Breck; *Orchis purpurea* in Kent). Many perennial species, including some of those species of our flora which are most markedly continental judged by their total distribution, show a remarkably wide scatter over Britain and even Ireland (cf. the annual Veronicas with *V. spicata*). A possible explanation of this will be suggested later.

Soil factors may next briefly be considered. Almost without exception our continental species are plants demanding soils of high base status, usually, of course, chalk or limestone soils. Thus, to take one example, the Atlantic grass-heath species of the Breckland (e.g. *Teesdalia nudicaulis*) occur on the leached acid sandy

soils, whilst the continental grass-heath species such as *Veronica verna* occur on unleached chalky sandy soils. This seems a reasonable correlation when we consider that the high rainfall and cool summers of an Atlantic climate favour the development of leached soils, and, of course, peat; whilst in a continental climate the high summer evaporation keeps soluble bases at or near soil surface and available even for shallow rooted species.

Factors of competition are clearly important in a consideration of the environment. The association of so many of our rare and local species with open habitats is too familiar to field botanists to need stressing. Steep chalk slopes and limestone cliffs have always been famous for their floristic richness. This emphasises the point that although we have a few woodland species with continental distribution, e.g. *Primula elatior,* the great majority of our continental plants are intolerant of shade, most commonly produced naturally by competitors, particularly shrubs or trees. Anyone who has been concerned with the conservation of rare species will know that the problems only begin when a fence is put round and 'protection' is given. Indeed one can take it as a general rule that our rare species cannot persist in the later stages of the natural succession of vegetation, which culminates normally in some type of woodland; that is in fact part of the reason for their rarity. This applies not only to the obvious case of the rare annuals of arable land, but also to herbaceous perennials of grassland (e.g., *Veronica spicata, Helianthemum* spp.) of fen (e.g. *Selinum Carvifolia, Liparis Loeselii*); and even, probably, to certain shrubs (e.g. *Sorbus* spp.) intolerant of effective forest cover.

A further striking feature of many continental species in W. Europe which is correlated with their wide disjunct distributions is the extent to which they are split up into local populations showing ecotypic adaptation (this was referred to by Prof. Tutin). Often the same species may be present in several of the possible types of non-wooded habitat on base-rich soil, e.g., sand-dune or brackish marsh, fen, chalk and limestone cliffs and slopes. The case of *Senecio campestris s.l.* (incl. *S. integrifolius* and *S. spathulifolius*) is interesting in this connexion. The rare Irish *Inula salicina* affords another striking example—this plant occurs in fens, on dry rocky slopes (C. Sweden), in brackish marshes (E. Denmark).

Time is short, so this must suffice as an outline of the Continental element in our flora. This Conference is, however, particularly concerned with *change.* What then do we know, and what can we reasonably guess, to be the history of change of this 'continental element'? Work such as that already outlined by Dr. Godwin, Mr. Walker, and Mr. West is fortunately supplying some of the answers, and enough concrete evidence has already accumulated to enable us to draw up a reasonable picture. It is clear that the Late-glacial period in what we now call the British

Isles, which lasted several thousands of years, offered an exceptional opportunity for the spread and success of many species intolerant of competition and demanding unleached soils of high base status. We know, for example, that *Polemonium coeruleum* and *Potentilla fruticosa* (both Northern Continental species with a very restricted British distribution to-day) occurred in the south of England in Late-glacial times. We can reasonably picture the Late-glacial countryside with considerable treeless areas of grassland or heath, and large areas of rich fen vegetation, in which many species of continental distribution type, so restricted in the British Isles to-day, must have been abundant.

There is, of course, no reason to restrict the entry and spread of our continental plants to the relatively forest-free Late-glacial, for throughout the Boreal period there must have been a considerable amount of more or less treeless terrain, not only of fen, but also locally where rocky ground prevented closed Pine forest. It is interesting to find that in precisely such areas in the coniferous forest in Scandinavia, for example, several of our most striking continental species occur to-day (e.g. *Hypochoeris maculata, Veronica spicata*).

The onset of the mild wet Atlantic climate would naturally be inimical to such species, not only directly, but also probably indirectly in further restricting, through increased competition from tall species, their available habitats, and also in causing more rapid leaching of the surface soil. It is possible, therefore, to picture the continental element being reduced to scattered refuges—sunny dry steep calcareous slopes, e.g.—where peculiar factors, particularly of topography, favoured them. Further, it is generally held that the separation of Britain from the Continent dates from the beginning of the Atlantic period, so that the entry of species from Europe would, on that account alone, be considerably retarded.

The Sub-Boreal period, coinciding roughly with the development of Neolithic clearings of chalk downs and Breckland, must have given to many of these plants a chance of secondary spread. This, I should like to suggest, may partly explain the intriguing phenomenon pointed out to me by Mr. Rose at the Society's previous Conference, viz., the absence or rarity of certain continental chalk grassland species in Kent and Surrey (e.g., *Astragalus danicus, Senecio integrifolius*). It is very difficult to believe that the present day factors, of climate, soil and competition, on the chalk of the North Downs are operating to exclude such species, and it is equally difficult to believe that the species were not in Late-glacial and Boreal times to be found in the S.E. corner of England. A possible explanation for their absence is that the clearance of the North Downs was much later, and for a long time less effective, than the early Neolithic clearance, for example in Wiltshire. In the Atlantic period the available refuges for the continental species were fewest in the south-east, where the softer chalk provided more rounded contours, so that the populations

of these species in the vicinity were reduced to a minimum, and those now absent have presumably failed to recolonise the now suitable chalk grassland. Thus we find that although Kent has an imposing array of continental species, the majority of those more or less confined to the S.E. corner of England are the light-seeded Orchids and Orobanches. It might seem therefore that annual species and perennials mainly dependent upon effective seed setting for survival are likely to exhibit distributions easily correlated with present-day climatic and other factors; whereas the distributions of the perennials with effective vegetative spread may well contain a much more obvious 'historic' factor. It is these perennial continental species which are to be found to-day in the 'refuge' habitats of N. or W. limestone; and it is these which show the striking and curious disjunct distributions.

On such a view we must, of course, assume that certain perennials, e.g., *Helianthemum Chamaecistus, Thymus Drucei,* must have had efficient means of spread on to chalk grassland as it arose, for they occur in most English counties to-day where the soil is suitable. It is in this kind of field that autecological studies are so badly needed; and I make no apology for ending this talk rather as Prof. Tutin has done, and as I seem to remember I did at the previous Conference, with a plea for some careful observation along these lines. Hundreds of amateur and professional botanists know our rare and local species and, I hope, treasure that knowledge; yet not one in a hundred undertakes the kind of study which we must have to solve some of these fascinating problems which I have touched on. Let me leave you with one concrete example. *Linosyris vulgaris* clings to the edge of a few western limestone cliffs in Britain, where it is literally 'between the Devil and the deep sea'. Why? Is it intolerant of competition? Presumably; but exactly why? Is it intolerant of grazing? Again, presumably; but again why? Is it intolerant of trampling? Apparently not; for at one locality where it is trampled but not grazed, it is said to have extended its area and actually come off the very edge of the cliff. If we knew the answers to these questions—or even a few of them—our speculations might be founded on firmer ground; and they are all questions which the local amateur is ideally placed to answer. Of course, I do not wish to leave you with the impression that it is merely the rare or local species which are interesting; but I have been dealing with such plants particularly in this talk, and it is also with them that one feels the problems might so easily be tackled—as indeed they must be tackled if we are interested in preserving them. If this Conference can really stimulate this kind of simple but time-consuming and long-term autecological enquiry, it will have made a real contribution to the progress of British Botany.

REFERENCE.

Matthews, J., 1937, Geographical Relationships of the British Flora, *J. Ecol.* **25**, 1-90.

This paper was discussed as follows:—

Prof. Webb suggested that in considering relict floras of any type, an important factor, which still needed much investigation, is the rate of turnover in the generations. Leaving aside annuals, perennial plants vary enormously in the average number of years that elapse between the germination of a seed and the displacing of the individual so produced by one of its own seedlings. His investigations at Killarney indicated that in the case of *Arbutus Unedo* there it was probably about a thousand years. It was probably long also in *Inula salicina,* which spreads largely by stolons. Assuming the establishing of the seedling to be usually the most critical stage for the survival of a species, it is clear that this rate of turnover is a primary factor in deciding how long a relict flora can persist under conditions that are no longer really suitable.

Mr. Rose remarked, in connection with Dr. Walters' observation on Breckland plants, that *Teesdalia nudicaulis,* an Atlantic species common on the leached soils of Breckland, was strongly maritime in S.E. England, being confined in Kent, for example, to shingle beaches near the South coast. In general, it seemed that the common plants of Breckland were Atlantic species of leached soils such as are usual in a cool oceanic climate (e.g. *Tillaea muscosa, Erodium cicutarium, Cerastium* spp., *Carex arenaria,* etc.), while the truly continental species of Breckland were mostly calcicole and were on the whole rare (e.g. *Carex ericetorum, Astragalus danicus, Silene Otites, Phleum phleoides*), occurring only where chalk lay near the surface. *Hypochoeris maculata* represented another case of the interesting type of double distribution shown by such a Continental species as *Veronica spicata* in Britain and commented upon by Dr. Walters. The *Hypochoeris* occurred as a small form on calcareous soils in Breckland and elsewhere in eastern England (Lincs., Beds., etc.) in a region of low rainfall, while a larger form of the species, perhaps comparable to the *hybrida* subspecies of *Veronica spicata,* occurs on limestone and basic soils at scattered points on the west coast of Britain —in two of them, interestingly, with subsp. *hybrida.*

Mr. Rose went on to say that, with regard to Dr. Walters' hypothesis that the present absence of such species as *Astragalus danicus* and *Anemone Pulsatilla* from the apparently ecologically suitable chalk downs of S.E. England was due to the persistence of forest in these areas through the period of general Neolithic clearance of the chalk elsewhere, he thought that attention should be drawn to apparent differences between the histories of the North and South Downs. The South Downs differed from the North Downs in showing abundant remains of Neolithic settlement and no evidence of ancient forest cover; yet these Downs also lacked the species mentioned. He felt that some other historical factor was involved in the cause of the absence of these species. He agreed with Dr. Walters, however, that *Senecio integrifolius* had a distribution supporting his theory, being extremely rare on the North Downs but very common on the eastern South Downs. The presence, too, of *Thesium humifusum* on the drift and forest-free plateau of the chalk of the extreme east of Kent, and its absence elsewhere in Kent, supported Dr. Walters' theory on one reading of the facts.

A CHANGING FLORA AS SHOWN IN THE STUDY OF WEEDS OF ARABLE LAND AND WASTE PLACES

Sir Edward Salisbury.

Dr. Godwin in his paper (see p. 59) has referred to the views I expressed twenty years ago referring to the end of the Pleistocene epoch. I wrote that "When we bear in mind the vast territory that was then gradually exposed and the considerable area of morainic deposits that must have fringed the extensive European ice front throughout the pleistocene glaciations, we cannot but realize that this must have been the heyday of the plants of open communities and may well have been the chief period, not only of their evolution, but also of their geographical extension".

Recent work on sub-fossil pollen in this country and elsewhere has tended to increase the probability of these views and if we examine the composition of the weed flora it is clear that the wide distribution of those species that appear to belong to no definite geographical component may well be an ancient feature. But even if we admit this, it is important to appreciate that changes in the plant population of open habitats has been in no small degree an accompaniment of man's activities which have created sanctuaries of reduced competitive pressure in areas where such might naturally be non-existent or rare. We recognize, of course, that in natural conditions the occurrence of landslides, of bare areas due to erosion, of wind-borne loess soils, of sand dunes, shingle beaches and the like, will always have provided habitats where pioneer species, intolerant of severe competition, could persist. In such habitats annual plants of ephemeral character inevitably disappear with the progress of the plant succession. Probably one of the earliest of human influences was the destruction of forests by fire, through palaeolithic man's desire to increase pasturage for the herbivorous animals he hunted, but with the coming of Neolithic man and a cultivation that was doubtless, like that of primitive peoples to-day, of a nomadic type, human influence became more important and from the earliest period when man sowed crop seeds till the advent of modern seed cleaning machinery, man has been sowing weeds. Thus the changes in his agricultural activities have inevitably been accompanied by changes in the weed flora, both in respect to their extent and in some degree with respect to their kind.

Wheat almost certainly came to Western Europe from the Mediterranean area and there seems little doubt that primitive agriculture was derived from that region. It is, therefore, of great interest to find among weeds of Neolithic Britain the Bluebottle or Cornflower, *Centaurea Cyanus*—a plant that is most

probably of oriental origin and possibly native in Italy, Greece and Cyprus, but is to-day a widespread cornfield weed, which has even reached America and New Zealand, though now far less abundant than formerly. The presence of the southern species of poppy, *Papaver Argemone,* in deposits of the Roman period, as at Silchester, is also perhaps suggestive. It is manifest, however, with regard to these plants of open habitats which are to-day mainly found in artificially created conditions, that whether we regard them as native or not is largely a matter of guesswork, unless we have evidence of the date of their introduction and they are exclusively found in artificially created conditions.

If we restrict ourselves to species that are almost certainly introductions, and assume that the earliest date on which they have been recorded is a rough measure of their arrival in this country, we are not surprised to find that, broadly stated, the earlier introductions were commonly European in provenance and known from the 17th century, whereas in the late 18th century and early 19th century we have the appearance of American species such as *Juncus tenuis, Impatiens fulva* (*I. capensis*), *Mimulus guttatus, Claytonia alsinoides.*

It is perhaps interesting to note that with the increasing provenance of garden species, more than one such has escaped to become a weed. I will only, however, in this connection, mention two species, both introductions into rock gardens in this country, and both now established in the wild and spreading. The first of these is the Creeping Willow herb, *Epilobium pedunculare,* which has already established itself in abundance in parts of the Lake District and in Snowdonia and elsewhere, competing very successfully with the native vegetation. The Creeping Speedwell, *Veronica filiformis,* which first appeared in Europe in southern France in the early '90s, bids fair likewise to become a pest and is now known to occur in at least 11 counties or vice-counties from Cornwall to Sussex in the south and as far north as Forfar (Fig. 15a). Moreover, I have seen patches of it flourishing in a permanent pasture in Gloucestershire that argues a capacity to tolerate a considerable measure of competition. The first point then we must recognize is that the weed flora in this country is continually being augmented and this augmentation involves change in the composition of the flora, both directly by reason of the new arrivals themselves and indirectly by their effect on the existing weed population, a process that is largely influenced by the geographical connections of the inhabitants of these islands.

It is too early to know whether air travel has materially influenced this process, but it may well be a factor that will play its part in future changes. The British flora is not an event but a process, that is continuing both with respect to accretions and diminutions.

A. *Veronica filiformis.*

B. *Galinsoga parviflora.* **First record: Richmond, 1860; Middlesex, 1862.**

C. *Claytonia alsinoides.* First record: 1834.

Fig. 15.

All these changes we are only able to follow with any degree of accuracy during the past hundred years, since when our flora has been more or less under observation and such changes are both in the direction of gains and losses. I have already referred to the way in which man unconsciously sows weeds in his crops and it is important to bear in mind to what degree this factor varies with the type of crop. It is sufficiently obvious to need no more than mention that even with the primitive screening of seeds that they adopted centuries ago, the standard of cleanliness, so far as imported seed is concerned, was greater with the larger and more easily cleaned grains such as cereals than with such "seeds" as those of grasses.

The data provided by our Seed Testing Stations bear this out. Out of 11,000 samples of Italian Rye Grass seeds examined by Johnson and Hensman prior to 1912, the average of impurities was 10%, and commercial samples had been examined by Borlase that contained as much as 68% of weed seeds. A conservative estimate which I made based on the returns for the first decade of this century suggests that at that time between two and six billion weed seeds were sown annually with grass and clover. If we accept Seebohn's estimate of 5 million acres under the plough at the time of the Doomsday Survey, this was about doubled by the end of the 19th century and to-day the area of arable land and temporary leys in England and Wales is over 13 million acres. Thus on the one hand the extent of the artificial habitats for weeds has been greatly augmented, possibly more than trebled during the past nine hundred years, whilst on the other hand increased purity of the seeds sown and the use of herbicides have tended towards their diminution.

Amongst changes which may be attributed to seed screening, none is more striking than the diminution in frequency of the Red Chamomile, *Adonis annua,* which was so abundant at one time in the cornfields of Kent, Surrey and Sussex, that it was regularly sold in Covent Garden market. To-day, as we know, it has become one of the rarest of our British weeds, persisting only in a few very restricted areas.

The Corn marigold, *Chrysanthemum segetum,* which was quite obviously a pest in the reign of Henry II, seeing that a special ordinance for the destruction of the Guilde Weed, as it was then known, was enacted, though still common, is far less so than half a century ago, a fact that many botanists now living can bear testimony to within their own experience.

The diminution of the Darnel, *Lolium temulentum,* and of the Corn Cockle, *Agrostemma Githago,* are both probably attributable to the same cause. There are references in Shakespeare and other writings to these two plants, which in Elizabethan times were both known as Corn Cockle, from which we can infer the abundance of these plants. To-day the *Lolium* is a rare plant and Corn Cockle is decidedly uncommon in areas where I, as a child, can recollect it as common. It is possible that the diminu-

tion of *Bupleurum rotundifolium* and *Delphinium consolida* in the East Anglian flora is attributable to this same cause.

The gains are more important than the losses, in number at least, if not in quality, and in regard to these, perhaps the most interesting aspect of the changes that have been brought about is in respect to the extent and rate of their spread.

We can obtain some indication of the provenance of our weed flora by considering those species, about 60 in number, which exhibit a marked geographical trend suggestive of their source of origin. Of these, practically 60 per cent. belong to the Southern component with a marked preponderance of the Continental Southern element. Here belong two of our groundsels, *Senecia viscosus* from southern Europe, which is probably native as far north as Belgium, and was first recorded in this country in 1660, and *Senecio squalidus* which first appeared in Oxford at the end of the 18th century and is a native of Sicily. To this component belong also *Adonis annua, Bupleurum rotundifolium, Iberis amara, Papaver Argemone, Silene anglica,* and *Specularia hybrida.* Most of the members of this geographical constituent we find had already been recorded in this country by the 16th and 17th centuries and the same is true of the continental component numbering about ten species. The 19th century introductions from Europe include *Cardaria Draba* which probably had its origin in South Eastern Europe, *Impatiens parviflora,* which comes from Russia, and *Veronica persica.* The late arrival of the last named in this country is perhaps rather surprising.

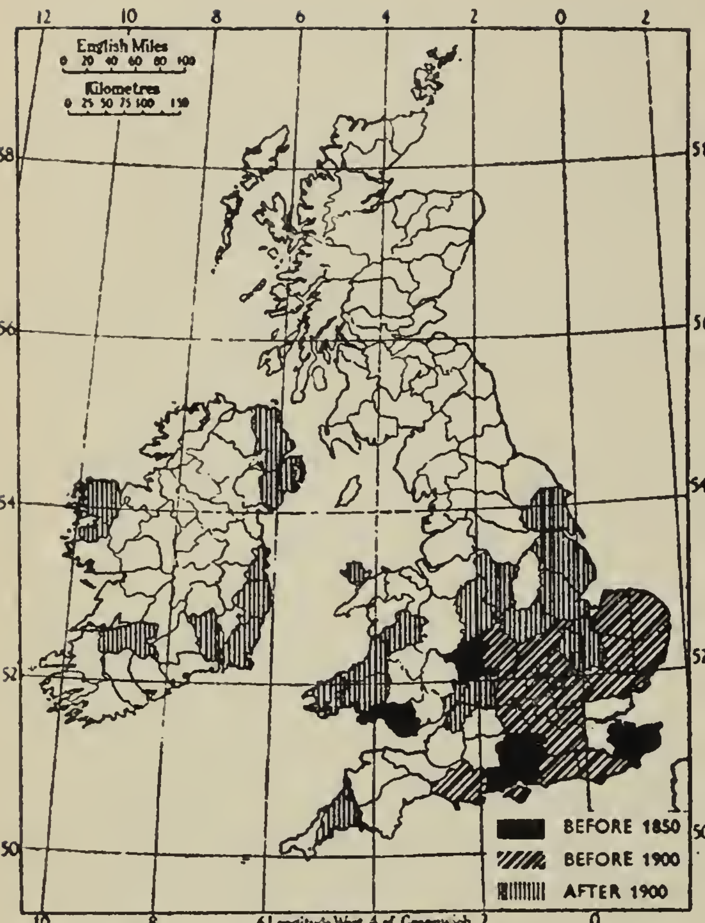
The American invasions are rather interesting. *Erigeron canadensis,* which came to England via Europe, was first recorded in 1690. Two others, namely, *Coronopus didymus* (1778) and *Juncus tenuis* (1795), have been with us since the end of the 18th century, but *Impatiens fulva* (1835), *Claytonia alsinoides* (1838) and *Claytonia perfoliata* (1852) (Figs. 15c & 16b) have probably been with us little more than a century, although the spread of the first was rapid, and of the last two delayed. Two composites, *Matricaria matricarioides* and *Galinsoga parviflora* (Fig. 15b) are of particular interest because of the lapse after their first recorded occurrences, during which they exhibited little if any spread, followed by comparatively rapid extension during recent years, a point which is worth elaborating.

The use of first records as an indication of the first appearance of a plant in this country is obviously but a very rough guide. But using these criteria for what they are worth, it would appear that there has been a broad correspondence between the extent of communication between areas and the frequency of plant introductions from them, such that human agency may have been a prime factor in determining the time of arrival. Perhaps, however, the most interesting feature of the changes in our weed population has been the diverse manner in which these various species have spread. *Cardaria Draba* was introduced into the Isle of Thanet in 1809, by human agency, actually as an outcome

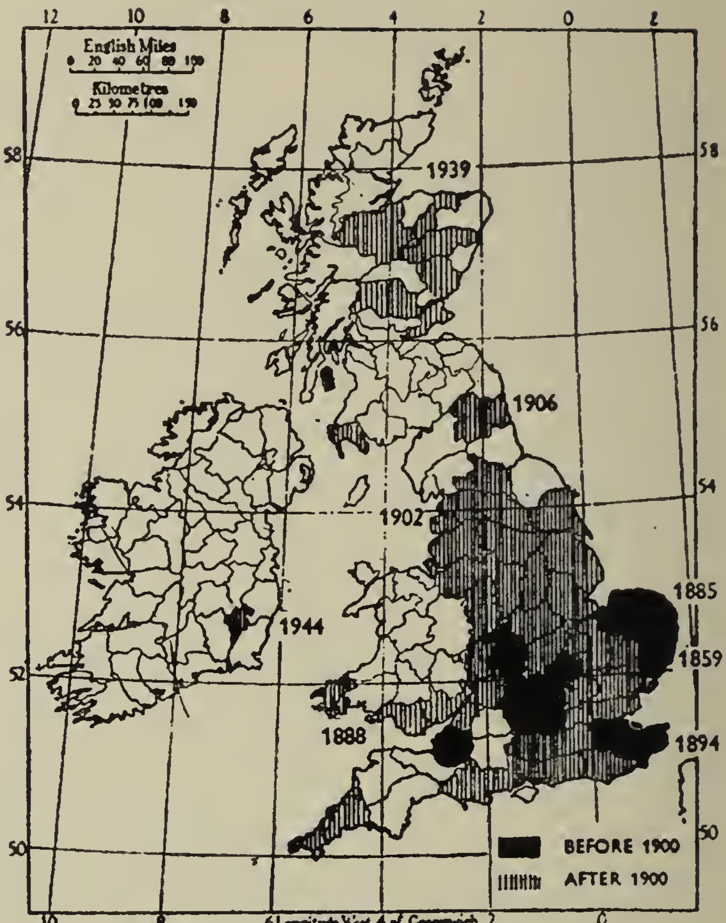
of the Walcheren expedition. Its spread since then has been steady and slow, a feature that is doubtless not unconnected with the comparatively large size of the seeds, which are not readily carried long distances, but nevertheless, its spread has been slower than the spread of some other propagules of equivalent weight and size (Fig. 16a). It should be added that germination tests show the viability of the seeds to be frequently high, but there is some indication that the vegetative spread by fragmentation of the roots, from which adventitious buds are freely produced, is in fact more frequently the means of its increasing range than by seedlings. This species had reached Dorset, Northamptonshire, and Warwickshire by the 'Seventies, but South-East Yorkshire, Derby and Ireland not till the early years of the present century. In contrast to this, we can cite the example of *Veronica persica,* which too has comparatively large seeds with no very obviously specialized mechanism of dispersal, but the rate of spread of *Veronica persica* showed a rapid rise after its first appearance in this country, just over one hundred and twenty-five years ago. Within a matter of 25 years it had become widespread in England and Wales and had already reached Ireland, but within fifty years of its first appearance in Britain it had probably extended almost throughout these Islands.

Matricaria matricarioides (*suaveolens*), a native of Oregon, was first recorded in this country in 1871 and prior to 1900 had been found as a casual in several widely separated areas including Cornwall, Caernarvon, Galway, Aberdeen and Lincolnshire. The fruits do not bear a pappus but are distributed in mud and, as the plant is with us essentially a wayside weed, the patterned tread of the motor tyre provided an exceptionally effective means for its dispersal. As an agency of dispersal, the motor car became effective after 1900 and, within twenty-five years, *M. suaveolens* had spread almost throughout England. I well recall the manner in which this species replaced *Matricaria inodora* on some of the bye-roads in Hertfordshire during the period of the first world war. For this species the determining factor in the time and rate of spread was the advent of a new and effective dispersal agent.

The history of *Galinsoga parviflora,* a native of Peru, is somewhat similar in the sense that this too came into Britain many years before it exhibited marked extension. First recorded as an escape from the Royal Botanic Gardens at Kew, it remained for years a purely local weed. Its dispersal is chiefly by wind, but the pappus is not highly effective, and by its spread on the bombed sites of London during the last world war I was able to show that its rate of travel was consistent with the hypothesis that wind dispersal depended mainly for its efficacy upon the upward convection currents and the rapidity in the rate of fall of the propagules. The latter determining the degree of probability that the propagules will be caught up by a wind current and carried a long distance. *Galinsoga* spread rapidly to other



A. *Cardaria Draba*. First record: Thanet, 1809.



B. *Claytonia perfoliata*. **First record**: Bedfordshire, 1852.

C. *Erigeron canadensis*. First record: Middlesex, 1690.

Fig. 16.

parts of the country during the war and this may well, in part at least, have been due to the bombing which sent many propagules to high levels and thus enabled winds to carry them away.

The spread of *Senecio viscosus* and *Senecio squalidus,* of *Erigeron canadensis* (Fig. 16c) and *Epilobium angustifolium,* are all alike instructive as illustrating species with highly efficient mechanisms for wind dispersal of their propagules, but which all exhibited a slow rate of spread followed by a rapid one which I suggest is a phenomenon analogous to the 'infection pressure' of epidemic disease. In each instance, the rapid spread followed upon local increase due to the artificial provision of suitable habitats. *Epilobium angustifolium* was a comparatively infrequent species until the augmented incidence of heath fires following upon the development of mechanical transport gave local impetus to the infection pressure. So too, *Senecio viscosus* had its impetus with the development of arterial roads between the two world wars and it was the extension of gravel pits beside these which gave the requisite density of propagule production that appears necessary to ensure rapid spread. The two species of wild Lettuce afford striking examples. *Lactuca virosa* was known in Britain from 1570 and *L. Scariola* from 1632, but it was the extension of gravel pits which here, as with *Senecio viscosus,* appears to have provided the requisite impetus and now both species are alike common occupants of waste ground over a wide area. The examples of Surrey and Hertfordshire will suffice to show the delayed action in their spread. Both were rare in Surrey in 1863. When Salmon's *Flora of Surrey* was published sixty-eight years later, *L. virosa* was cited as rare and *L. Scariola* as very rare, but both have alike become frequent or locally common during the past twenty years. *Lactuca Scariola* was a very rare plant in Hertfordshire a century ago. It was still of the same status forty years ago. In the early twenties of the present century it began to increase and is now a common plant of waste ground. It seems quite clear from these and other instances that a certain density of occurrence which implies a minimum concentration of propagules is requisite before the infective pressure becomes such that an epidemic develops. In some aquatic species of which *Elodea canadensis* is an example there is evidence that the period of abundance may be followed by a period of population decline, but as to the *modus operandi* we are almost completely ignorant although some of the facts are at least suggestive.

This paper was discussed as follows: —

Mr. Ash enquired whether the spread of *Veronica persica* was the cause of the decrease of *V. agrestis.* Sir Edward Salisbury replied that he thought this very doubtful, since the two species occurred in somewhat different habitats and were therefore not usually in full competition. *V. agrestis* is a weed of rich garden soils where *V. persica* is not common.

Dr. Baker asked what the speaker would expect to be the pattern of spread in *Veronica filiformis*, as he understood that this species is seed-sterile in the British Isles as a result of its self-incompatibility and reproduces vegetatively. He suggested that a comparison with a self-compatible annual such as *V. persica* might be very illuminating. Sir Edward Salisbury replied that *V. filiformis* was planted in gardens and when thrown out it increased vegetatively, but some fertile seeds are produced.

Mr. Rose asked if the case of *Lactuca Scariola* and *L. virosa*, and their recent "explosive" increase (whereas they had previously been rare) could be compared with that of *Chamaenerion* (*Epilobium*) *angustifolium*. Sir Edward Salisbury said that they provided good examples of "infection pressure" which could be compared with that shown by *Epilobium angustifolium*.

Mr. Lousley said that wind, as mentioned by the speaker, was not the only vector involved in the spread of *Galinsoga parviflora*. From 1915 it has been abundant in nursery garden ground at Eastfields, Mitcham, from which bedding plants are distributed to shops and gardens in Streatham and elsewhere. He had sometimes seen *Galinsoga parviflora* in pots of plants exhibited for sale in Streatham shops and it frequently appeared in gardens after they had been bedded out with *Pelargonia*, etc. The species thrived in nursery gardens elsewhere and had appeared in tubs planted with ornamental shrubs in Ware, Hertfordshire, to give only one example. He thought that the evidence suggested that distribution from nurseries was an important factor in its spread. Sir Edward Salisbury replied that many aliens were distributed in more than one way, and this might well apply to *Galinsoga parviflora*.

Prof. Webb said that there were interesting comparisons to be made in the success and manner of dispersal of plants of this type between Ireland on the one hand and Britain on the other. *Epilobium angustifolium*, though fairly widespread in Ireland, is nowhere really abundant or aggressive; perhaps it has not yet built up enough "infection pressure". In Ireland, where motor traffic is of less importance, *Matricaria matricarioides* is primarily a farmyard plant, and Praeger has shown that it is rapidly spread in mud on boots, and has in this way reached the western islands. *Senecio squalidus* is, among the Irish aliens, the plant most dependent on railways for its transport. Sir Edward Salisbury, in reply, said that it was noteworthy that rubber soles on footwear had been shown to be as effective in spreading *Matricaria matricarioides* as rubber motor tyres.

Mr. Milne-Redhead observed that the use of maritime shingle as ballast on railway tracks appeared to be responsible for the introduction of seaside plants to some inland counties. For instance, *Cerastium tetrandrum* and *Cochlearia danica* had recently been found on railways in Bedfordshire. He suggested that more attention should be given to plants growing between the metals of railway lines, and the plants found recorded.

Dr. Haskell said that he would like to add a few comments to what had been said about *Galinsoga parviflora*. A month or two after the John Innes Horticultural Institution moved from Merton to Hertford, he went back to the old site and was surprised to find that the experimental plots were covered with a dense mat of *Galinsoga*. This in spite of the fact that the grounds had been carefully hand-weeded and hoed regularly for about 25 years. In the last few years the plant has become an absolute pest in the gardens of nearby Tooting. When the Institution first moved to Bayfordbury in 1949 no *Galinsoga* was found, but in 1951 a plant appeared on one of the plots which contained rootstocks brought from Merton. It must have been introduced with the roots transplanted.

Dr. Haskell went on to say that, with Mr. Marks, he had recently examined the chromosomes of *G. parviflora*, and also of *G. ciliata*, which was recorded in 1939 by Mr. Brenan, and recently described by Mr. Lousley. They found that *G. parviflora* is an old tetraploid acting as a diploid, while *G. ciliata* has twice as many chromosomes, and is an old octoploid behaving as a tetraploid. From peculiarities of the chromosomes they concluded that *G. ciliata* is not directly derived from *G. parviflora*. In view of the interest in the spread of these species he wished to draw attention to the opportunity a few years hence of comparing the spread of two members of a polyploid series. They grew the two species in the glasshouse, and they germinated with difficulty in John Innes compost. However, seeds that had dispersed themselves on the bench cinders germinated vigorously, much to the chagrin and alarm of the head gardener, who was terrified of the weed establishing itself.

THE RECENT INFLUX OF ALIENS INTO THE BRITISH FLORA

J. E. Lousley.

The part played by species introduced by human activities in changing the flora of Britain is one of outstanding importance. Additions to the flora of our islands from this source far outnumber those from others, and, moreover, the quantitative expansion of such species is often spectacular and detrimental to the plants already here. Previous papers have dwelled on certain aspects of this subject; it is my task to consider it generally.

First, I must make it clear that I am using the word "alien" in its widest and now most common use. Aliens are species believed to have been introduced by the intentional or unintentional agency of man. They are thus contrasted with native plants, which are those which are believed to have either been in Britain before man, or to have immigrated without his aid by using their natural means of dispersal. (The latter also includes the rare cases where species or varieties may have arisen *de novo* in this country.) From the wealth of material at my disposal in considering aliens, I propose to deal mainly with the ways in which they are brought into the country and distributed by human activities, and then with the stages by which some of them become quasi-permanent members of our flora.

Looking back over the last quarter of a century—a period well within the botanical experience of many of us—it is surprising how many changes have occurred through the spread of aliens. For example, *Senecio squalidus* L., which is now so abundant on bombed sites and waste places over much of England and Wales, was still regarded as rare in 1927, by which year I had seen it in only three places. *Epilobium pedunculare* A. Cunn., which is the subject of Miss Davey's exhibit (see p. 164), now so thoroughly established in the hills of Ireland, Wales and northern England, was then unknown as a British plant. *Epilobium adenocaulon* Hausskn., of which the discovery and spread has been described by Mr. Ash (see p. 168), was not detected until 1935, though it had then no doubt been naturalised for some time. To compile detailed accounts of the spread even of these three species within so recent a period is now no easy task, and those who have attempted it have found gaps difficult or impossible to fill. In past centuries botanists were less numerous and less mobile and the difficulty of tracing the history of introduced plants at that time is even greater.

Means of Introduction.

If the progress of aliens is to be adequately recorded, it is plain that they must be studied from the time of their first arrival in Britain. An essential step towards this is to be aware of the agencies by which plants which are natives of other countries are introduced. I have only time for a very brief review of the known or suspected sources of aliens, and for a few examples of each.

Table 1.

Agencies by which Foreign Plants may be introduced.

A. Foreign Cultivated Plants intentionally introduced for Use or Ornament.

1. Grown for commercial purposes. This includes seeds and fruits brought in for manufacture (e.g. cereals, drugs, Soya beans).
2. Garden plants grown for (a) ornament, (b) culinary purposes, (c) medicinal use.
3. Grown in botanic gardens.

B. Foreign "Weeds" introduced involuntarily.

1. *With* grain for (a) milling, (b) use in breweries or distilleries, (c) poultry food.
2. *With* seeds for cultivation—(a) farm crops—cereals, clover and vetches, lucerne, sainfoin, flax, carrots, etc., (b) garden seeds.
3. *With* trees, shrubs and herbaceous plants imported to be grown from roots (now rare owing to restrictions).
4. *With* feeding stuffs for human or animal consumption—(a) oil seeds, (b) Soya beans, (c) food for cage birds and game, (d) fodder.
5. With wool imported for manufacture or manure.
6. With skins, hides and furs.
7. With imported timber.
8. In ballast.
9. From shipwrecks.
10. With packing materials.
11. On people, vehicles (including aeroplanes) and living animals.

It is useful to distinguish between the plants which are brought in deliberately and those which come in accidentally as "stowaways". The latter are unwanted impurities in imported materials or arrive as unobserved attachments to people, vehicles or animals. These attachments are often seeds of species with means of dispersal well adapted to the vectors by which they arrive. On the other hand, the cultivated plants are deliberately selected by man from the world flora for other qualities, often including ability to grow in our climate.

An interesting example of a cultivated plant grown for commercial purposes is *Phormium Colensoi* Hook. f. which is naturalised on cliffs in the Isles of Scilly where an attempt was made to grow it as New Zealand Flax. The allied *P. tenax* Forst. is said to be similarly naturalised in the Isle of Man. Garden plants which have become naturalised vary, as one would expect, in different parts of the British Isles according to the climate. Thus *Gunnera chilensis* Lam., which is unable to survive severe winter conditions, thrives in the Channel Islands and west Ireland. *Helxine Soleirolii* Req. is common in the south and south-west of England. The American species of *Aster* and *Solidago* have a wider range. Scotland has a peculiar selection of naturalised garden plants, including those of Tayside which was described in 1869 as a perfect "nursery of aliens", which it still is. *Lupinus nootkatensis* Sims, from the island of Nootka near Vancouver, is well known from the shingle of the Dee and the Tay, but it is even more abundant in the Orkneys. There, on the island of Mainland, it is said to have locally even exterminated the heather. *Senecio Smithii* DC., from the Straits of Magellan, is naturalised in Caithness and the Shetlands.

A culinary garden plant now well established is *Tragopogon porrifolius* L. which grows on sea-walls, clay meadows and roadsides in Essex and Kent about the mouth of the Thames. The best known example of a plant which has spread from a botanic garden is *Galinsoga parviflora* Cav., which was first recorded outside Kew in 1861. Oxford, Edinburgh and Glasnevin have also been responsible for the introduction of aliens which have persisted outside the gardens for a period. The list of species anciently cultivated for medicinal purposes which are now well naturalised is a long one. It will be sufficient to cite *Rumex alpinus* L. of which the roots were used in the treatment of ague and, incidentally, the leaves for wrapping butter.

Turning now to the plants introduced involuntarily, the most important source is that of the grain aliens. These may be found about flour mills, such as those at Felixstowe and Bristol (Sandwith, 1933), or near breweries and distilleries. Siftings and sweepings from the Wandsworth Distillery were responsible for a list of 154, mostly foreign, species published in 1863 (Brewer, 1863). The Bass and Worthington Breweries were the main sources of 267 species recorded from Burton-on-Trent in 1932 and 1946 (Curtis, 1931; Burges, 1946). Sweepings and inferior grain used as poultry food are the origin of many aliens found about chicken runs.

Imported seed for cultivation now contains far fewer aliens than formerly, thanks to improved cleaning methods and the vigilance of seed-testing stations. In these days seed-corn brings in few foreign plants, but in crops of clover and vetches, *Vicia varia* Host and allied species are increasingly common, while *Centaurea solstitialis* L. still appears in lucerne, and occasionally in sainfoin. During and after the war, carrot seed was respons-

ible for many American aliens, including *Solanum sarachoides* Sendtn. which is now thoroughly established on light soils in the eastern counties. Foreign weeds sometimes appear in gardens from imported seed of garden plants sold in packets.

It is difficult to find proof of the importation of aliens with living plants for cultivation but the possibility of their coming in with young trees for afforestation or plantations is very obvious. It is possible that *Maianthemum bifolium* (L.) Schmidt and *Scutellaria hastifolia* L. have come to this country in this way.

Various feeding stuffs imported for human and animal consumption bring in many aliens. Oil seeds at Olympia sidings, Selby, and Soya Beans at Harefield, Middlesex, have been responsible for interesting records. Seeds sold as food for game- and cage-birds commonly produce grasses such as *Phalaris canariensis* L., *Setaria viridis* (L.) Beauv. and *Panicum miliaceum* L., Hemp, *Cannabis sativa* L., and the Composite, *Guizotia abyssinica* Cass.

Imported wool contains much vegetable matter, including seeds and fruits which the sheep collects in its foreign pasture. In Yorkshire (Lees, 1941) and Tweedside (Hayward & Druce, 1919) the plants growing in the vicinity of woollen mills derived from the cleaning of the wool have been the subject of interesting studies. More recently Dr. Dony has been working on the aliens which appear in Bedfordshire after the use of "shoddy" as manure in cultivated fields. He will be dealing with this in the next paper (see p. 160). The importance of shoddy is that it is a means of distributing wool aliens about the country, and, for example, *Medicago hispida* Gaertn. and *Erodium moschatum* (L.) L'Hérit. in parts of Kent probably have their origin from this source. *Acaena anserinifolia* (J. R. & G. Forst.) Druce is an example of a thoroughly naturalised wool alien. The importation of exotic seeds with skins, hides and furs is similar in that many of the species have hooks or spines on the seeds or fruits by which they become attached to the animal in its pasture. F. A. Lees and others record a long list of species brought in in this way found at Gibson's Tannery and Exley's Fellmongery at Meanwood near Leeds (Lees, 1941).

Rough imported timber is likely to be a source of aliens, since felled trees may well have seeds adhering to their bark from herbs on which they fall when felled, or over which they are dragged. Examples are the North American *Carex vulpinoidea* Michx. and *C. Crawfordii* Fern. which I found growing along the side of a track made of rough timber laid across a chalkpit near Farnborough, Kent.

Ballast I will discuss a little later, but shipwrecks (not necessarily of ships bound for this country) provide an interesting possibility which may explain the British distribution of some well established aliens. My attention was drawn to this in 1936 when I saw a line of *Coriandrum sativum* L. extending for per-

haps 300 yards on the edge of the Marram Grass at Sandwich Bay in Kent. These plants had come from seed from a wreck on the Goodwins the previous winter. Although the species is one which has not become established, the observation demonstrated that seed of a non-maritime plant could germinate after being carried for a few miles in the sea. I have since experimented with the fruits of the South American *Rumex cuneifolius* Campd. which has grown on sand-dunes at Kenfig and Braunton Burrows, on opposite sides of the Bristol Channel, since at least 1934 and 1929 respectively, in places so remote that it is unlikely to have been brought there by any ordinary human activities (Fig. 17). The buoyancy of these fruits and the viability of the seeds was found to be hardly affected by immersion in sea-water for 68 days.

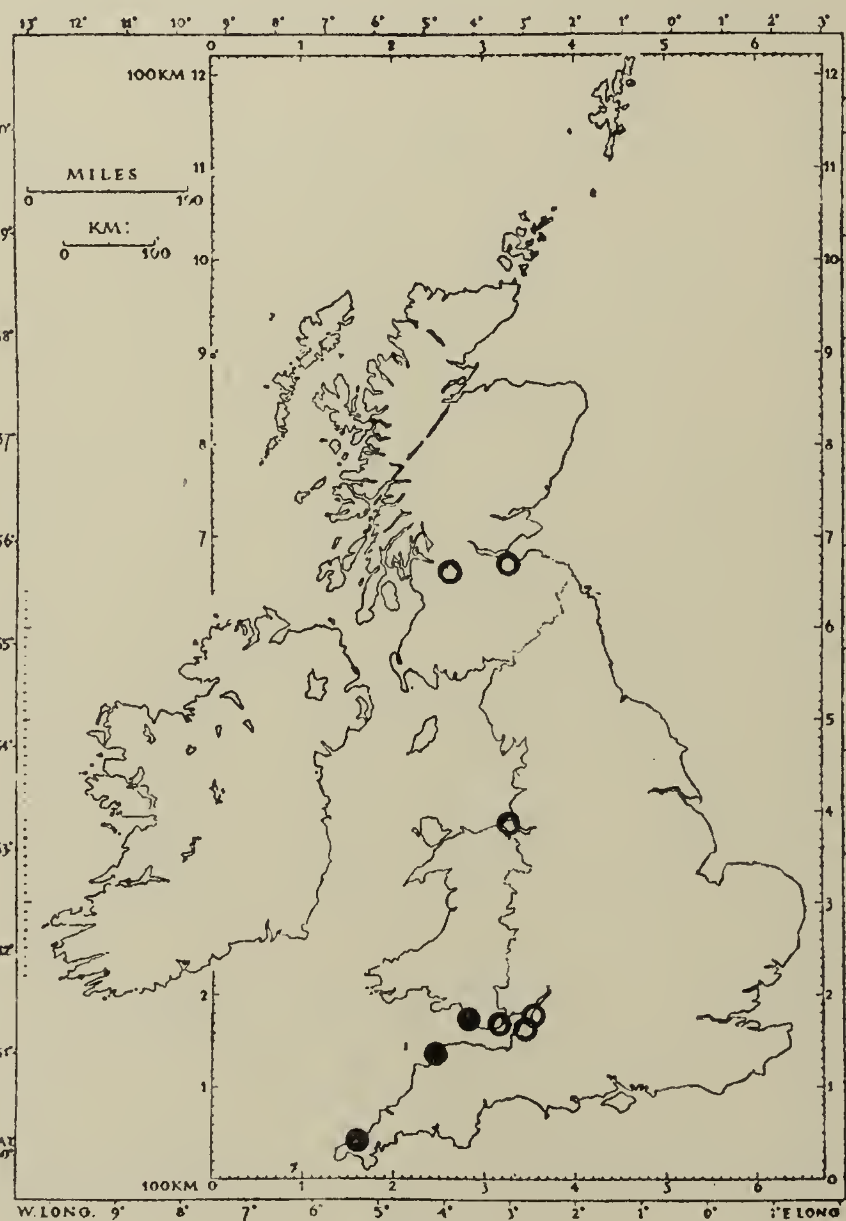


Fig. 17.

Rumex cuneifolius Campd.

The three localities where the species is thoroughly naturalised on coastal dunes are shown with solid dots: other occurrences are indicated by circles.

With acknowledgment to "The New Naturalist" for use of the base map.

It is therefore possible that *Rumex cuneifolius* originated at Kenfig (Plate IIIa) and Braunton from seed which floated away from a shipwreck. Both colonies could have come from a single wreck in the vicinity of Lundy Island. On the other hand, the locality at Hayle, which is also on sand-dunes, seems more likely to have originated in another way, since other aliens grow with it.

There is even less evidence of the importation of aliens by the means I am about to mention, though it is reasonable to suppose that they have considerable importance yet to be proved. *Salsola pestifera* Nelson appeared (and disappeared) twice in the City during the war in places where packing materials had been dumped. It is now thoroughly established on rubbish dumps about the Metropolis. Of plants brought in by travellers or vehicles there appears to be no direct evidence, but people arriving from abroad must surely bring occasional seeds or fruits adhering to their clothing. Inspection of the trouser turn-ups of men coming to this country by sea or air might provide evidence of a form of introduction which may have been going on since primitive man brought seeds on the skins he used for clothing. Vehicles used overseas are another likely source, and botanists using their cars for foreign tours could help by making careful examination of the wheels and upholstery on return. Air transport offers new possibilities and it might be worth while keeping British airports under observation for alien plants. (Although hardly comparable, it is of interest that 214 living insects have been collected from 121 aircraft arriving at Shannon Airport (O'Rourke, 1950)).

All these agencies by which plants are introduced from abroad are subject to changes according to the habits and commerce of the people of Britain, and these changes are reflected in the plants recorded by botanists. *Carum Carvi* L. and *Rumex alpinus* L. became widely naturalised in Scotland because former generations of Scots were fond of Caraway and suffered from ague, but it is unlikely that modern crofters would take the trouble to introduce them. Many similar instances might be given of changing fashions in garden and medicinal plants, but I should like to draw particular attention to one aspect which deserves further investigation. Hylander (1943) has published a most illuminating account of the flora of the Swedish parks and shown that they contain an assemblage of French and German species (some of them critical) which appear to have come in with mixtures of grass seeds, etc., when the parks were laid out during the second half of the nineteenth century. In this country such species as *Poa Chaixii* Vill., *Festuca heterophylla* Lam., and *Luzula luzuloides* (Lam.) Dandy & Wilmott are recognised as plants of the parks prepared around mansions during the affluent Victorian times. It is likely that a special study would show that the list is much more extensive, and the recently discovered *Dactylis Aschersoniana* Graebn. is probably another example.

Seeds brought in as impurities by commerce vary according to the trade. Until after the middle of the last century, the great majority of our aliens were from Europe and the Near East, but during the last hundred years an increasing share have come from North and South America, Africa and Australasia. The early high proportion of natives of the Mediterranean is to-day almost maintained by species from that area, which have become naturalised in other lands, such as Australia, from which seeds of their descendants are now brought to Britain. Present currency difficulties are reflected in the reduced number of aliens coming from South America as compared with before the war.

One very big change obvious in comparing contemporary records with those in some of the older books is the modern almost complete absence of ballast aliens. It was formerly the custom for vessels engaged in the export of coal and other heavy commodities to load gravel, sand, rock or soil at the foreign port and to return "in ballast". At some ports, such as Cardiff, this material when unloaded was used to build up low-lying marshy ground; at others, such as the Tyneside towns, it was just heaped up in "ballast hills" on the coast. In either case it was often a paradise for those in search of unfamiliar plants. Useful accounts are available of the plants found at Cardiff (Storrie, 1886), where the use of water ballast in colliers had caused the quantity of material deposited to decrease greatly by 1886, and also of those on the coast of Northumberland and Durham (Hogg, 1867). Ballast material was taken inland for the repair of railways and some of the ballast plants, such as *Linaria minor* (L.) Desf. and *Senecio viscosus* L., spread in this way in north-east England.

War is one of the most important factors in causing changes in the sources of introduced plants. During the recent war North American weeds were frequently brought here in the materials supplied by the United States and Canada (Libbey, 1945). *Solanum sarachoides,* already mentioned as well established in the eastern counties, dates from this phase in our history. War also causes great movements of vehicles and equipment. Although direct evidence is lacking, it is not unlikely that seeds were brought back on the wheels and tracks of trucks and tanks used overseas. It is possible that *Carex vulpinoidea* was brought by the Canadians to Tadworth, Surrey, in this way. But plants spread by armies, *polemochors* as Mannerkorpi has called them (Luther, 1948), are mainly dispersed with horse fodder. In the past, plants, such as *Bunias orientalis* L., were moved right across Europe with army fodder. Earlier wars probably had a considerable influence on our flora (*Cardaria Draba* (L.) Desv. is said to have been introduced from the Walcheren expedition) but our forces in the 1939-1945 period had little or no use for horses. The Germans and Russians invading Finland during the same period introduced a number of new plants as Luther (1948) has shown.

The Dispersal of Aliens by Commerce in Britain.

From this review of the means by which foreign plants are brought into Britain it will be evident that the very great majority arrive as seeds as accidental impurities in cargoes coming by sea. The first opportunity of studying them is at the ports, and at different times the flora of the docks at Barry and Cardiff (Smith & Wade, 1926, 1927), Avonmouth and Bristol (Sandwith, 1933), Falmouth, Charlestown and Par (Thurston, 1929), Newport, Isle of Wight (Long, 1932), Southampton (Brenan, 1947), Colchester (Brown, 1916, 1927, 1939, 1940), Felixstowe, Hull (Wilson, 1938), and Leith (Fraser & McAndrew, 1904) have been investigated. Plants growing at docks usually stand little chance of survival for more than a very short period, and they are usually isolated by pavement and buildings from more permanent habitats. The value of their study rests in their significance as samples of the species arriving in this country and available as potential additions to our flora after further distribution with human aid. Their floristics faithfully record changes in our imports and vary from port to port according to the nature and sources of the trade.

From the ports the cargoes are taken away by rail or canal, and to a lesser extent by road. Railways offer the best opportunities for study, as seeds drop out through the bottom of the wagons when they are being shunted or as their contents are unloaded, so that goods and shunting yards are often rich in introduced plants. When they are situated in country districts, the aliens have especially good opportunities of spreading away from railway premises. Some cargoes are transported in barges on rivers and canals, and where they are unloaded at small quays, such as Forstal near Aylesford, Kent, or (formerly) Virley, near Colchester, Essex, seeds are likewise spilled in unloading and may become established. The vicinities of mills, factories and warehouses to which the materials are consigned offer further opportunities of study.

Some imports become distributed over the country to farms and gardens where there may be opportunities for the establishment of the included foreign seeds. Others go to towns, and the aliens with them may find their way to municipal rubbish dumps. These are usually situated on the outskirts of the towns, or, in the case of the larger cities, in the country. Thus much of London's rubbish is dumped on the Essex banks of the Thames, while some goes by rail to such rural spots as Sundon in Bedfordshire. The London tips have been examined fairly regularly (Melville & Smith, 1928; Kent & Lousley, 1951, 1952) and it is clear that the flora owes much of its variety to less obvious origins, such as the sweepings from druggists' stores and the food of cage birds. Most of the plants which appear persist only for a very short time, but there are opportunities for the spread of suitable species.

Naturalised and Established Species.

The relatively few species which are able to persist out of the large number distributed over the country in these various ways are those which find habitat and climatic conditions which suit them. They must also be able to compete with some measure of success with the plants already present. It is only when they have succeeded in doing this for a sufficient number of years to have survived the normal variations in the extremes of our climate that they should be regarded as naturalised or established. I would suggest twenty-five years as a reasonable period of qualification for this purpose.

It is convenient to draw a distinction between the use of the terms '"naturalised" and "established", although some writers treat them as synonymous. Naturalised species are those which persist in *natural* or *semi-natural* communities where they compete with native plants. While some, like *Epilobium pedunculare* and *Tetragonolobus maritimus* (L.) Roth, seem able to withstand full competition, most of them are restricted to open communities such as those of coastal sand-dunes or the shingle of rivers and lake-margins. *Rumex cuneifolius* at Kenfig (Plate III) and *Lupinus nootkatensis* at Ballater are examples. Established species on the other hand are restricted to *man-made habitats,* like *Senecio squalidus* on bombed sites, railway banks, and arable fields, and *Ranunculus muricatus* L. in the bulb-fields of Scilly. The success of both naturalised and established species in spreading away from their point of introduction depends on their means of seed dispersal. The rate at which extension takes place varies greatly between species, and it sometimes varies also from time to time in the same species.

To illustrate the varying dependence of naturalised and established plants on man-made habitats I have selected seven recent examples. They are arranged to form a series from those at present restricted to artificial habitats to those found in more or less natural communities.

The first two are restricted to arable fields. *Thlaspi alliaceum* L. was first found at Ripper's Cross near Hothfield, Kent, in May 1923 and the farmer then said that he had known it for many years (Plate VI). It was so thick in the field that the soil was red with the seeds, and it was estimated that an average of 79,768 seeds per square yard were produced over a field of about 15 acres (Ware & Chambers, 1923). Its early flowering time is likely to favour its persistence as a weed in crops and yet, so far as we know, it has not extended its ground in thirty years from the place where we will see it to-morrow. (It was found by R. M. Payne in 1951 near Maldon, Essex, where it must have been an independent introduction).

In contrast, *Ranunculus muricatus,* which was also first recorded in 1923, in the Isles of Scilly, is spreading rapidly there (Plate IIIB). It is abundant in many of the bulb-fields, and last year Mr. John Raven found it on the mainland of Cornwall near

PLATE III.

A. *Rumex cuneifolius* Campd. Kenfig Dunes, Glamorgan, August 26, 1938.

B. *Ranunculus muricatus*. L. In bulb-field, St. Mary's, Isles of Scilly, May 28, 1938.

Photos by J. E. Lousley.

Poltesco. It is likewise an early fruiting species and the spines on the achenes probably assist in their distribution. As a casual in Britain, it has been found as a grain-alien at Wandsworth and several ports, as a probable wool alien on Tweedside, and on the Tyneside ballast hills. It was established near Prestwick, Lancashire from 1875 to 1893, but I know of no later records from there. A native of the Mediterranean region, it is now naturalised on the east and west coasts of North America and in Australia and New Zealand.

It is too early to claim the grass *Vulpia megalura* (Nutt.) Rydb. as established, but it is likely that it was overlooked before its discovery in 1945. It was found then by the railway at Grimston, Norfolk, by Mr. E. L. Swann, who suggested that it had come in with "Lease-Lend" carrot seed. In 1946, and again in 1947, it was found near railways in Bedfordshire and last year in great quantity on waste ground near Hoo, in Kent. The species is native on "sterile soils" on the west side of North and South America. In England it has only been found on disturbed ground where it does not enter into full competition with native plants.

Rapistrum rugosum (L.) All. has now passed into communities which, although not natural, are free from constant disturbance from human activities. It has long been a frequent grain alien at docks and railway sidings, where it sometimes persisted for a few years when conditions allowed. At Holywell, Eastbourne, it grew below the cliffs from 1874 until at least 1886. Near Aylesford, Kent, it was "bidding fair to become established" 57 years ago, and it is still plentiful there and elsewhere down the Medway to Upnor. It is now abundant along the sea-wall of the Thames estuary east of Gravesend and on Stone Marshes. On the other side of that river, it is common in South Essex—for example at Barling near Southend it is abundant in arable fields and also on the sea-wall. About Felixstowe, in Suffolk, it grows in various habitats. Thus, on the east coast *Rapistrum rugosum* is thoroughly established and not entirely dependent on habitats kept open by human activities. It occurs also in many other places in Britain, though usually as a casual.

Another crucifer, *Bunias orientalis* L., has gone a stage farther, and become established in natural communities in full competition with native plants. Also a grain alien, it is found fairly frequently on waste ground, rubbish tips, roadsides, etc. About Sunbury Lock, in Surrey, it has persisted since 1880. But it is on the chalk that it attains its highest status. Thus it still occurs in *Brachypodium pinnatum* grassland and in a woodland ride on Clandon Downs, Surrey, where Dunn described it as naturalised in 1894. Near Farleigh it grew in close chalk grassland until the little down was ploughed during the war. Elsewhere in Surrey, Buckinghamshire and Oxfordshire, it is very much at home on the chalk.

Fig. 18.

Tetragonolobus maritimus (L.) Roth in Britain. The localities where the species is known to have persisted in competition with native plants are indicated with larger dots. The dates are those of the first evidence and an arrow indicates that the species still persists in the locality shown.

My final examples are of two species which have persisted for a good many years in competition with the native flora. The first is *Tetragonolobus maritimus* (L.) Roth, which appears in some works as *T. siliquosus* (L.) Roth and has also been placed under *Lotus*. In Britain, as in the neighbouring continental countries, it grows both on calcareous and on clay soils (Fig. 18). These soils all have a high base content. It was first naturalised on the chalk near Winchester where it was discovered in 1875 and it persisted until at least 1916, after which date I have been unable to trace further records. In Gloucestershire it was found on the Oolite in 1924 by the Rev. E. Ellman, who was informed by the owners of the rough pastures in which it grew that they had known it for about 20 years. They said that some of the land had been cultivated for potatoes and manured with barley refuse. In Berkshire it was found between Streatley and Basildon in 1912, and is still in the district, and near Henley it continues to thrive on a small chalk down where it was discovered in 1924.

The other apparently permanent stations for *T. maritimus* are on clay about the mouth of the Thames. At Birchington it has persisted since 1910, on the Sheppey cliffs since 1926, and at West Mersea since 1930. At Hockley, near Southend, it was not discovered until 1947 but here it grows partly in arable land which

the farmer is reclaiming from rough pasture where it has evidently been growing for many years. These localities are shown on the map by large black circles; places where the species has a shorter history, by dots. The suggestion that it was introduced with barley refuse at the Gloucestershire station receives some support from the fact that it has been found at Burton-on-Trent, where much barley is used for brewing. The Hockley farmers have a tradition that it was planted by Dutch settlers. The deep and thick underground parts of the plant render it extremely difficult to eradicate by ploughing, and the British habitats so closely resemble those in which it is found as a native over most of Europe, that it seems likely to become a permanent member of our flora.

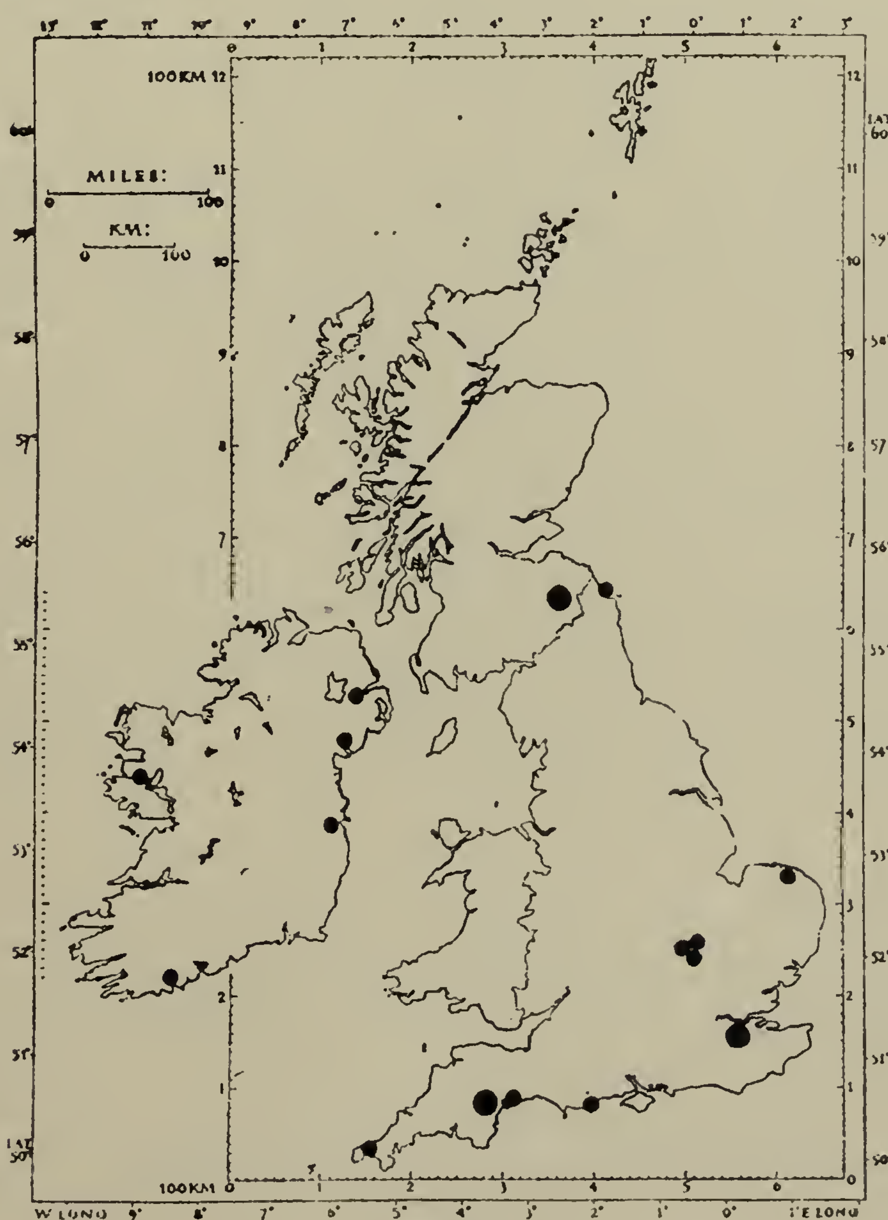


Fig. 19.

Acaena anserinifolia (J. R. & G. Forst.) Druce.

The large dots indicate the three localities where the plant is known to be thoroughly established in competition with native species. Other occurrences are marked by smaller dots.

With acknowledgment to "The New Naturalist" for use of the base map.

Lastly, I should like to give an example of a wool alien. *Acaena anserinifolia* (Forst.) Dr., a very variable species, is a native of Australia and New Zealand where the fruits, each crowned with four long barbed spines, are found in samples of wool delivered to the Appraisement Stations (Church, 1947). They have also been found in wool received at the Tweedside mills which, no doubt, is the origin of the great colonies which have been established on shingle and the rocky banks of the Tweed below Melrose since at least 1908 (Fig. 19). In Devon, about Haytor Down, the species has been naturalised since 1901 and is now found growing under bracken. There is an old wool industry in the neighbourhood.

Distribution of the seeds in shoddy explains how it got to Bedfordshire, where I have seen it in three gravel pits and on a bank by Langford sidings where shoddy is unloaded from the trucks. It was probably in shoddy that it was brought to Mereworth Woods near Wrotham, Kent, where it is very abundant and grows in at least two places a mile apart. It was first collected here in 1937 by C. A. Rylands, who observed that it grew with "Rosebay, Ground Ivy, Wood Sage, Centaury, etc." (Herb. Kew).

Although imported wool is the agency by which *Acaena anserinifolia* has been brought to the localities where it is most thoroughly naturalised, it is important to realise that, as with many other plants, it can come into these islands in more ways than one. At Hayle (Cornwall), Studland (Dorset) and in Ireland it is likely to have started as a garden outcast, and the same probably applies to Kelling Heath in Norfolk. I do not know how it got to the sands of Holy Island off the Northumberland coast but it could have come attached to the clothing of a visitor who had been on Tweedside. At Kew there is a specimen of a plant grown from seed found in a sample of New Zealand Chewing's Fescue at the Cambridge Seed Testing Station—so imported agricultural seed is another possible source from which it may yet appear.

Native and Alien Species.

At this point it is interesting to reflect on how a botanist arriving in this country in 1952, and completely ignorant of their history here, would treat these seven species. He might fairly argue that before man arrived there were no cultivated fields, and that therefore *Thlaspi alliaceum* and *Ranunculus muricatus* must be aliens. On similar grounds he would arrive at the conclusion that *Vulpia megalura* was an alien because it is restricted to the vicinity of railways and wharfs. This conclusion would be strengthened by the fact that its main centre of distribution was separated from England by the Atlantic and the land of America. *Rapistrum rugosum* and *Bunias orientalis* would leave him in doubt and he would probably argue about them with his confrères indefinitely. The fact that the main centre of distribution of *Acaena anserinifolia* is in Australasia would save him from calling this a native—or if he did, he would have to accept a very remark-

able example of disjunct distribution. But *Tetragonolobus maritimus* would mislead him completely—he would have no reason to doubt from its distribution and ecology that he was dealing with a native of Britain.

Our own knowledge of our flora is rather like that of the hypothetical botanist just mentioned. The written history of British plants goes back only for four centuries, and herbarium material for a much shorter period. It seems to me that we pay too much attention to the fact that some species have been known for the greater part of this short history, when deciding whether to treat them as natives or aliens. Much valuable evidence is available from our increasing knowledge of their distribution, ecology and biology here and abroad, and careful use of this might well provide indications that some of the plants generally accepted as natives were in fact introduced by human activities. For example *Cynodon Dactylon* (L.) Pers. at Marazion was quite likely introduced from the nearby, and then active, port of Penzance prior to its first record of 1688, just as it has been introduced into so many other places since. *Geranium pyrenaicum* Burm. f. which was first recorded by Hudson in 1762 has since shown the characteristic rapid expansion of aliens into man-made habitats, just as it has in other parts of Europe where it is no longer regarded as native.

Another line of investigation, likely to bring interesting results, is that of more critical examination of introduced plants of species already in the country. In studying congregations of plants of undoubted alien origin at the docks and elsewhere, one cannot help being impressed by slight differences in the species one knows best. I have noticed this particularly with *Rumex crispus* L. and *R. obtusifolius* L. of which I happen to have studied the variation in British populations. In these plants the variants occurring as aliens are often very different from those seen elsewhere, although the differences are sometimes difficult to describe. It seems likely that the strains already in Britain may be descended from those introduced on more than one occasion in the past, and that other strains are now being brought in and may become established. In *Rumex obtusifolius,* we have the known examples of the established alien subspecies *transiens* and *sylvestris.*

Similar alien variants exist in *Chenopodium* and *Polygonum,* while in studying the Bedfordshire wool aliens with Dr. Dony we have often been impressed with minor differences between them and examples of the same species we see elsewhere. Thus *Erodium cicutarium* (L.) L'Hérit. occurs as a form with finely dissected leaves which is readily recognisable but seems to have no special name, and perhaps does not deserve one. *Medicago minima* (L.) Bartal, is often found as the variety *recta* but there are other variants different from our seaside plant. Similarly, in fields where "Lease-Lend" carrot seed has been sown a host of strange forms of *Solanum nigrum* L. appear.

The Classification of Aliens.

I would like to turn now to consideration of the terms used for the classification of aliens according to their status. Just as the terms "native" and "alien" are arbitrary and their application in individual cases is often a matter of opinion, so the terms used for status depend on personal judgment to an even greater extent. Nevertheless a classification is essential for any adequate discussion of the subject and an attempt must be made to recognise broad categories capable of useful and practical application. Unfortunately, the terms at present in use have been subject to so much confusion that it is essential for any author making use of them to supply his own definitions (e.g. Dunn, 1905).

The first serious attempt to group British plants on this basis was that of H. C. Watson in his *Cybele* published in 1847. Here he defined his terms Native, Denizen, Colonist and Alien. In 1870 in his *Compendium* he considerably amended his definitions, and added a fifth class—the Casuals. These are the terms in common use in this country at the present time. The weak spot in his scheme is the inclusion of the loosely defined and heterogeneous class of Aliens which he evidently used to account for species which would not fit in elsewhere. From his examples it is impossible to get a clear idea of the limits he intended to impose on this category.

On the Continent there have been interesting attempts to classify aliens according to their dependence on human activities. Rikli, about 1903, introduced the term Anthropophytes for plants dependent on Man, and these he divided into Anthropochores, being those brought from outside the area by human agency, and Apophytes, or those already in the area in natural habitats which appear in man-made stations (Rikli, 1904). His work was elaborated by Thellung, and the detailed classifications which followed are of great value in drawing attention to important aspects of the relationship of aliens to the native flora and to human activities (Naegeli & Thellung, 1905; Thellung, 1912. 1915, 1918-19). Unfortunately, the practical application of these schemes is limited, since even in small areas it is often difficult or impossible to decide to which of the categories a good many of the species belong. Thus, as Thellung recognised himself, his Ergasiophygophytes belong also in part to his Ephemerophytes and in part to his Neophytes. French botanists still make effective use of Thellung's terms, but some of them are so long and difficult to pronounce that they are unlikely to be acceptable to English workers. Simmons (1910) and Linkola (1916) have each produced amendments of the Rikli-Thellung scheme in connection with northern European plants.

In this country the most useful and practical recent analysis of the flora according to status is the one set out by Hyde and Wade in *Welsh Flowering Plants* (1934). They give five grades as follows: —

Grade A. Undoubted natives.
Grade B. Doubtful natives.
Grade C. Introduced species naturalised in natural habitats.
Grade D. Introduced species established in man-made habitats.
Grade E. Adventives.

Grade "A" is equivalent to Watson's "Natives", and Grade "E" to his "Casuals", though for the latter Watson's term is very much to be preferred to the ambiguous "Adventives" which is often used (e.g. by Thellung) in a much wider sense. Grade "B" of Hyde and Wade includes "Colonists" and "Denizens" (though not all that have been so-called) but it makes no attempt to differentiate between "Doubtful Natives" growing in man-made habitats, and those in more or less natural communities. Grades "C" and "D" together comprise what Watson would have called "Established Aliens". The following table sets out the approximately equivalent grades of the Hyde and Wade, Watson, and Rikli-Thellung schemes.

TABLE 2.
COMPARISON OF TERMS OF STATUS.

HYDE & WADE, 1934.	H. C. WATSON, 1868. (approximate equivalents)	RIKLI-THELLUNG (approximate equivalents)
A. Undoubted Natives	Natives	Natives (Autochtones)
B. Doubtful Natives	Denizens (in natural habitats) and Colonists (in man-made habitats)	(Not separately included)
C. Introduced Species Naturalised in Natural Habitats	Established Aliens	Neophytes
D. Introduced Species Established in Man-made Habitats		Epoekophytes (including Archaeophytes which are weeds of cultivation in the country since early times)
E. Adventives	Casuals	Ephemerophytes

Watson's terms are too vague to serve modern requirements, but I would suggest that with slight amendment of their definitions and by adding two extra terms, we could introduce a classification which would serve our purpose better than the present one. This might be as follows:—

A. NATIVES. Species believed to have been in Britain before man, or to have immigrated without his aid by using their natural means of dispersal, or to have arisen *de novo* here.

1. NATIVES. e.g. *Corylus Avellana* L., *Calluna vulgaris* (L.) Hull.

B. DOUBTFUL NATIVES. Species with a long history in Britain but which are suspected of having been introduced by human agency.

2. DENIZENS. Species growing in natural or semi-natural communities and not dependent for their persistence on human disturbance of the habitat.
   e.g. *Myrrhis Odorata* (L.) Scop., *Mentha longifolia* (L.) Huds. (This is Watson's term in a slightly restricted use).
3. COLONISTS. Species which grow only in habitats created and maintained by human activities. These are mainly weeds of cultivation restricted to arable fields and disturbed ground.
   e.g. *Papaver Rhoeas* L., *Agrostemma Githago* L. (This is a considerably restricted use of Watson's term, and equivalent to Thellung's ARCHEOPHYTES).

C. ALIENS. Species believed to have been introduced by the intentional or unintentional agency of man.

4. NATURALISED ALIENS (or NEOPHYTES—the "new citizens" of Rikli). Introduced species which are naturalised in natural or semi-natural habitats.
   e.g. *Epilobium pedunculare* A. Cunn., *Rumex cuneifolius* Campd., *Acaena anserinifolia* (J. R. & G. Forst.) Dr., *Tetragonolobus maritimus* (L.) Roth.
5. ESTABLISHED ALIENS (the EPOEKOPHYTES of Rikli). Introduced species which are established only in man-made habitats.
   e.g. *Senecio squalidus* L., *Thlaspi alliaceum* L., *Ranunculus muricatus* L.
6. CASUALS (the EPHEMEROPHYTES of Rikli). Introduced species which are uncertain in place or persistence, i.e. not naturalised or established.
   e.g. *Guizotia abyssinica* Cass., *Phalaris canariensis* L., *Ricinus communis* L., *Rapistrum hispanicum* (L.) Crantz.

In this scheme the six grades are arranged in sequence of the apparent decreasing degree of permanence of the included species as members of our flora. It will be seen that grades 4 and 5 are complementary to grades 2 and 3, and, in fact, the latter have to be included only because our knowledge is incomplete. Thus the denizens are in reality either natives or naturalised aliens,

but they have been known here so long that we have, for most of them, no means of deciding to which they belong until further facts can be made available. Similarly the colonists may be really native plants which have changed their habitat (apophytes), or established aliens, but many of them belong to the large class of cornfield weeds of some of which no native home is known. The status of individual species may move up in the scale: thus in Britain as a whole *Rapistrum rugosum* was a casual up to fifty years ago; it is now an established alien and may soon become a naturalised alien. It is also important to notice that terms used for status must not be transferred from accounts of one area to those of another. To return to the example just given, *Rapistrum rugosum* is still only a casual in Wiltshire and many other counties, in spite of its higher status in Kent, Essex, and Suffolk. When considering the country as a whole it is customary to give only the highest grade attained, but where space allows it is preferable to make fuller statements such as: "Established alien in v.-cc. 15, 16, 18, 25; casual elsewhere". Even from this, the fact that the alien may take more than one grade within a single vice-county is not apparent.

For small areas, it may be possible to use the formula introduced by Praeger in 1911 in his account of the flora of Clare Island (Praeger, 1911, 1934), which is valuable in drawing attention to the three-fold factors involved in status. He adopted Dunn's definition of a "Native Plant", which is "A species is only held to be native in a natural locality to which it has spread by natural means from a natural source" (Dunn, 1905). This involves (1) the origin of the plant; (2) the means by which it reached its present habitat and (3) the nature of the habitat. Praeger's formula employs "N" to indicate "uncontaminated conditions", whether of source, dispersal or habitat, and thus a fully native plant is represented as NNN. "Contaminated conditions" are represented by "*", and by this means eight combinations of the three conditions can be shown. Thus *Guizotia abyssinica* which has been imported from the East, and the seeds dumped by man on a rubbish dump would be shown as ***. If we accept *Acaena anserinifolia* as an Australian plant, brought by rabbits from nearby orchards to the natural habitat where we will see it to-morrow in Mereworth Woods, the formula will be *NN. Such an analysis has very interesting possibilities but it is extremely difficult to apply.

In this paper I have tried to show that a serious study of the very large number of aliens with which Britain is "bombarded" annually is likely to produce interesting results of considerable scientific value. In particular, we need to know much more about the less obvious means by which plants are introduced, and we require a more detailed knowledge of the introduced strains of species already here. A reassessment of the status of species already in our flora is overdue and for this all available

information, and especially the knowledge of ecologists and plant geographers, should be collated. Provided such work does not divert attention from the study of supposedly "native" species, it offers great scope for a better knowledge of "Our Changing Flora".

(I should like to record my indebtedness to Dr. J. G. Dony and Dr. E. F. Warburg for their help in reading the manuscript of this paper and to Mr. B. T. Ward for preparing many of the lantern slides with which it was illustrated.—J. E. L.)

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Time was not available for discussion of this paper; otherwise DR. HESLOP-HARRISON and DR. ANDREAS would have drawn attention to the interesting introduction of *Oxycoccus macrocarpus* (Ait.) Pers. into Holland, which is believed to have been due to a shipwreck. Dr. S. J. van Ooststroom, of the Rijksherbarium, Leiden, has kindly supplied the following information based on Van Dieren's accounts (1933, *De Levende Natuur*, **38**, 141-144, 213-214). The story was told to Van Dieren by an inhabitant of the island of Terschelling and must have taken place about 1840. It seems that two wreckers found a wooden tun washed ashore and took this up into the dunes for examination. When opened, the contents of the tun were found to consist of more or less rotten berries which were abandoned by the disappointed finders. These were American Cranberries which had been part of the cargo of a ship and they soon became established on the Terschelling dunes. The islanders found them so palatable and easy to grow that their cultivation developed into an industry which is still an important source of revenue for the people of the district.

WOOL ALIENS IN BEDFORDSHIRE
(Exhibit)

J. G. Dony.

This exhibit was based on a study of 112 species of wool aliens found in Bedfordshire during the past six years. About twenty other species found with them were excluded as there was some doubt as to whether they were introduced with wool. Wool aliens are introduced into the South Midlands with grey shoddy, the refuse of wool-combing sheds, which is used somewhat extensively as a manure on light market-gardening soils (Plate IV). It is used in varying quantities in various other parts of the country and it is hoped that alien species introduced with it many receive more attention from botanists. Railway sidings in agricultural areas might be searched profitably, in the first instance, for species of *Medicago* and *Erodium* which are usually an indication that shoddy is being used in the neighbourhood. In arable fields *Xanthium spinosum* L., a prominent species, is usually a good indicator that other wool alien species may be present. Many wool aliens are cosmopolitan species, which have apparently been introduced into the wool producing countries with sheep or as fodder crops. The following comparative tables illustrate this feature clearly.

Average imports of wool into United Kingdom, 1948-1951, million lbs.

Australia	364	
New Zealand	189	
		77.1%
South Africa	60	8.2%
India	14	
Pakistan	13	
		3.7%
Peru	4	
Chile	4	
Argentine	5	
Falkland Is.	4	
		2.3%
France	21	
Belgium	8	
		4%
Turkey	4	0.6%
Irish Republic ...	10	1.4%
Other Countries	15	2.1%

Presumed region of origin of 112 Bedfordshire wool alien species.

Australasia	32	(28.6%)
South, East and Tropical Africa	13	(11.6%)
Middle East	2	(1.8%)
South America ...	12	(10.7%)
North America ...	5	(4.5%)
Mediterranean ...	34	(30%)
Europe	10	(8.9%)
Near East	3	(2.7%)
Far East	1	(0.9%)

A few wool alien species have become established in gravel pits in the neighbourhood of arable fields where shoddy has been used. These, *Acaena anserinifolia* (J. R. & G. Forst.) Druce, *Trifolium*

PLATE IV.

Photos by J. E. Lousley.

Heaps of "shoddy" ready for spreading in a field at Flitton, Bedfordshire, in which wool aliens appear regularly, and (below) close-up of part of one of these heaps, showing seeds, fruits and other vegetable material embeded in the wool.

angustifolium L. and *Juncus pallidus* R.Br., are all perennials. There is no evidence of annuals becoming persistent weeds of arable land. Hayward and Druce (1919), however, recorded *Solanum nigrum* L. and *Chenopodium album* L. as wool aliens from Tweedside. Both are common enough weeds in market-gardening areas, and alien varieties should be looked for when there is an apparent increase in these weeds after shoddy has been used.

It is difficult to name some of the material, as various genera, e.g. *Medicago* and *Juncus,* which include wool alien species, are badly in need of revision. Many of the species are late-flowering in this country and some do not flower at all. This may be due to the fact that market gardeners keep their fields clear of weeds during the summer, and field botanists do not normally see the alien plants until the autumn, when the crops have been gathered. Similarly railway staff keep their sidings much clearer in summer than they do later on. On the other hand the late-flowering may be due to length of day. This is certainly the case with *Tagetes minuta* L., *Bidens bipinnata* L., and some species of *Chenopodium,* which have been observed in this country in a non-flowering condition throughout the spring and summer and to flower regularly at the same time in the autumn. Also, the fact that wool aliens grow from seed ripened in the Antipodes may have a bearing on the problem.

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The list of wool aliens observed in Bedfordshire between 1945 and 1951 given below must be regarded as only tentative. It is given pending publication of a more complete list with accounts of those species not previously recorded for Britain. I am grateful to all those who have helped with the identification of material.

BEDFORDSHIRE WOOL ALIENS.

Brassica Tournefortii Gouan	Mediterranean
B. griquana N. E. Br.	South Africa
Carrichtera annua (L.) Aschers.	Mediterranean
Lepidium hyssopifolium Desv.	Australasia
Malvastrum peruvianum (L.) A. Gray ...	South America
Malva parviflora L.	Mediterranean
M. nicaeensis All.	Mediterranean
Lavatera plebeia Sims	Australasia
Triumfetta annua L.	Tropical Africa
Erodium Botrys (Cav.) Bertol.	Mediterranean
E. obtusiplicatum (Maire, Weiller & Wilczek) J. T. Howell	Mediterranean
E. cygnorum Nees	Australasia
E. moschatum (L.) L'Hérit.	Mediterranean
E. cicutarium (L.) L'Hérit.	European

Monsonia brevirostrata R. Knuth ...	South Africa
M. biflora DC.	South and East Africa
Medicago laciniata (L.) Mill.	Near East
M. praecox DC.	Mediterranean
M. minima (L.) Bartal.	European
var. *recta* (Desf.) Burnat	Mediterranean
M. hispida Gaertn. (*M. lappacea* Desr.)	Mediterranean
var. *denticulata* Willd.	Mediterranean
var. *apiculata* Willd.	Mediterranean
M. arabica (L.) Huds.	European
M. tribuloides Desr.	Mediterranean
M. ciliaris Krocker	Mediterranean
M. Aschersoniana Urban	Near East
Melilotus sulcata Desf	Mediterranean
Trifolium glomeratum L.	European
T. angustifolium L.	Mediterranean
T. tomentosum L.	Mediterranean
T. resupinatum L.	Mediterranean
T. subterraneum L. var. *oxaloides* (Bunge) Rouy	Mediterranean
Acaena anserinifolia (J. R. & G. Forst.) Druce	Australasia
Myriophyllum verrucosum Lindl. ...	Australasia
Ammi majus L.	Mediterranean
Daucus glochidiatus (Labill.) Fisch., Mey. & Avé-Lall.	Australasia
Calotis cuneifolia R.Br.	Australasia
C. dentex R.Br.	Australasia
Xanthium spinosum L.	South America
X. Strumarium L.	South America
Bidens bipinnata L.	South America
B. pilosa L.	South America
Tagetes minuta L.	North America
Madia sativa Molina	South America
Matricaria occidentalis Greene	North America
Cotula australis (Spreng.) Hook. f. ...	Australasia
Centaurea melitensis L.	Mediterranean
C. calcitrapa L.	Mediterranean
Carthamus lanatus L.	Mediterranean
Carduus tenuiflorus Curt.	Mediterranean
Senecio arenarius Thunb.	South Africa
S. lautus Soland. ex Willd.	Australasia
Schkuhria pinnata (Lam.) Cabrera ...	South America
Datura Tatula L.	Near East
D. ferox L.	Far East
Nicotiana suaveolens Lehm.	Australasia
Physalis ixocarpa Brot.	North America
Nicandra physaloides (L.) Gaertn. ...	South America
Marrubium vulgare L.	European
Amaranthus retroflexus L.	European

A. Thunbergii Moq.	South Africa
A. chlorostachys Willd.	South America
A. Dinteri Schinz var. *uncinatus* Thell.	South Africa
Chenopodium pumilio R.Br.	Australasia
C cristatum (F. Muell.) F. Muell. ...	Australasia
C. carinatum R.Br.	Australasia
C. Probstii Aellen	Australasia
C. auricomiforme Murr. & Thell. ...	Australasia
C. giganteum Don	Australasia
C. album L. var. *bernburgense* Murr. ...	? European
Monolepis Nuttalliana Greene	North America
Atriplex Eardleyae Aellen	Australasia
A. Muelleri Benth.	Australasia
A. semibaccata R.Br.	Australasia
Rumex Brownii Campd.	Australasia
Juncus pallidus R.Br.	Australasia
J. australis Hook. f.	Australasia
Panicum capillare L. var. *occidentale* Rydb.	North America
P. laevifolium Hack	South Africa
Dactyloctenium radulans (R.Br.) Beauv.	Mediterranean
Tragus racemosus (L.) All.	Mediterranean
T. australiensis S. T. Blake	Australasia
T. Berteronianus Schult.	Tropical Africa and Tropical America
T. koelerioides Aschers.	South Africa
Phalaris minor Retz.	Mediterranean
P. paradoxa L.	Mediterranean
Eleusine indica (L.) Gaertn.	Middle East
E. multiflora Hochst. ex A. Rich. ...	Tropical Africa
Rynchelytrum villosum (Parl.) Chiov. ...	Tropical and South Africa
Agrostis avenacea J. F. Gmel.	Australasia
A. lachnantha Nees	South Africa
Polypogon monspeliensis (L.) Desf. ...	European
Eragrostis cilianensis (All.) Vign. Lut.	European
E. parviflora (R.Br.) Trin.	Australasia
E. Dielsii Pilg.	Australasia
Chloris truncata R.Br.	Australasia
C. virgata Sw.	Tropical America
Cynodon hirsutus Stent	Australasia
Danthonia sp.	Australasia
Diplachne fusca (L.) Beauv.	Middle East
Bromus molliformis Lloyd	European
B. rubens L.	Mediterranean
B. unioloides Kunth	South America
B. madritensis L. var. *ciliatus* (Guss.) ..	Mediterranean
Trachynia distachia (L.) Link	Mediterranean
Lolium temulentum L.	Mediterranean
Hordeum Hystrix Roth	Mediterranean
H. leporinum Link	Mediterranean

EPILOBIUM PEDUNCULARE IN BRITAIN
(Exhibit)

Miss A. J. Davey.

Epilobium pedunculare A. Cunn. is a native of New Zealand which has successfully established itself in the British Isles during the past forty years. In early records this plant appears as *Epilobium nummularifolium* A. Cunn., probably owing to the use of the first edition of Cheeseman's *Flora of New Zealand,* in which *E. pedunculare* appears as a variety of *E. nummularifolium* A. Cunn. in agreement with Hooker's *Handbook of the Flora of New Zealand* (1864). In the second edition of Cheeseman's flora (1925), *E. nummularifolium* R. Cunn. ex A. Cunn., *Precur.,* 1839, and *E. pedunculare* A. Cunn. are described as distinct species. The most obvious distinguishing feature is that the fruit of *E. pedunculare* is glabrous; that of *E. nummularifolium* is 'clothed with a fine ash grey pubescence'. It is now acknowledged that those British herbarium specimens and records which have been checked, agree with *E. pedunculare.** For information on this point, the author is indebted to the late Mr. A. J. Wilmott and to Mr. Bangerter of the Natural History Museum, Mr. Hyde of the National Museum of Wales, and Dr. Lloyd Praeger. In correspondence, Dr. Praeger says "I have every reason to think that the Irish *E. nummularifolium* is in every case *E. pedunculare.* Since the two plants were separated, the former has not been definitely recorded from Ireland and the older records which cannot be checked referred, I believe, to *E. pedunculare*". The earlier Scottish records were supplied by Mr. John R. Lee.

E. pedunculare A. Cunn. was first recorded in Great Britain in 1908 as a weed in the gardens of Elmete Hall, Roundhay, Leeds, where it had been introduced with shrubby Veronicas from New Zealand to nursery beds, brick walls and waterside stones (A. E. Bradley, F. A. Lees). Also in 1908, there occurs the only record for Wiltshire where the plant was found outside a garden near Preshute Bridge in disturbed ground, and, subsequently, wild in a hedge associated with *Sagina procumbens.* Prior to 1930, records are few and scattered. They include: Ardrishaig, Kintyre (101†), P. Ewing, 1911; Uckfield, E. Sussex (14), H. Roberts, *Rep. Bot. Soc. & E.C.,* **4** (1916) (the only record for this vice-county); Hauxty Wood and Alston, Cumberland (70), "possibly from a garden"; although common in gardens in the Newcastle district, the plant does not persist in the wild state (K. B. Blackburn, 1925); Tubney Wood, Berkshire (22), Mrs. Skewer, *Rep.*

*This has also been urged repeatedly by Dr. W. A. Sledge—see *The Naturalist* for **1947**, 157-8; *Irish Nat. J.*, **10**, 56-57, etc.—Editor.

†Numbers in brackets are those of the Watsonian vice-counties.—Editor.

Bot. Soc. & E.C., 8 (1929); Carding Mill Valley and Church Stretton, Shropshire (40), *Rep. Bot. Soc. & E.C.*, 8, (1929).

From about 1932 onwards, records are more numerous and the plant became common and abundant in certain areas (fig. 20). There began a period of increase and rapid spread which has continued up to the present time. The records show that *E. pedunculare* A. Cunn. is a successful colonizer in the western and west coastal parts of Great Britain and the maritime counties of Ireland. These are regions of high rainfall and high humidity. The plant ranges from sea level to high altitudes, where cloud and mist are prevalent, succeeding

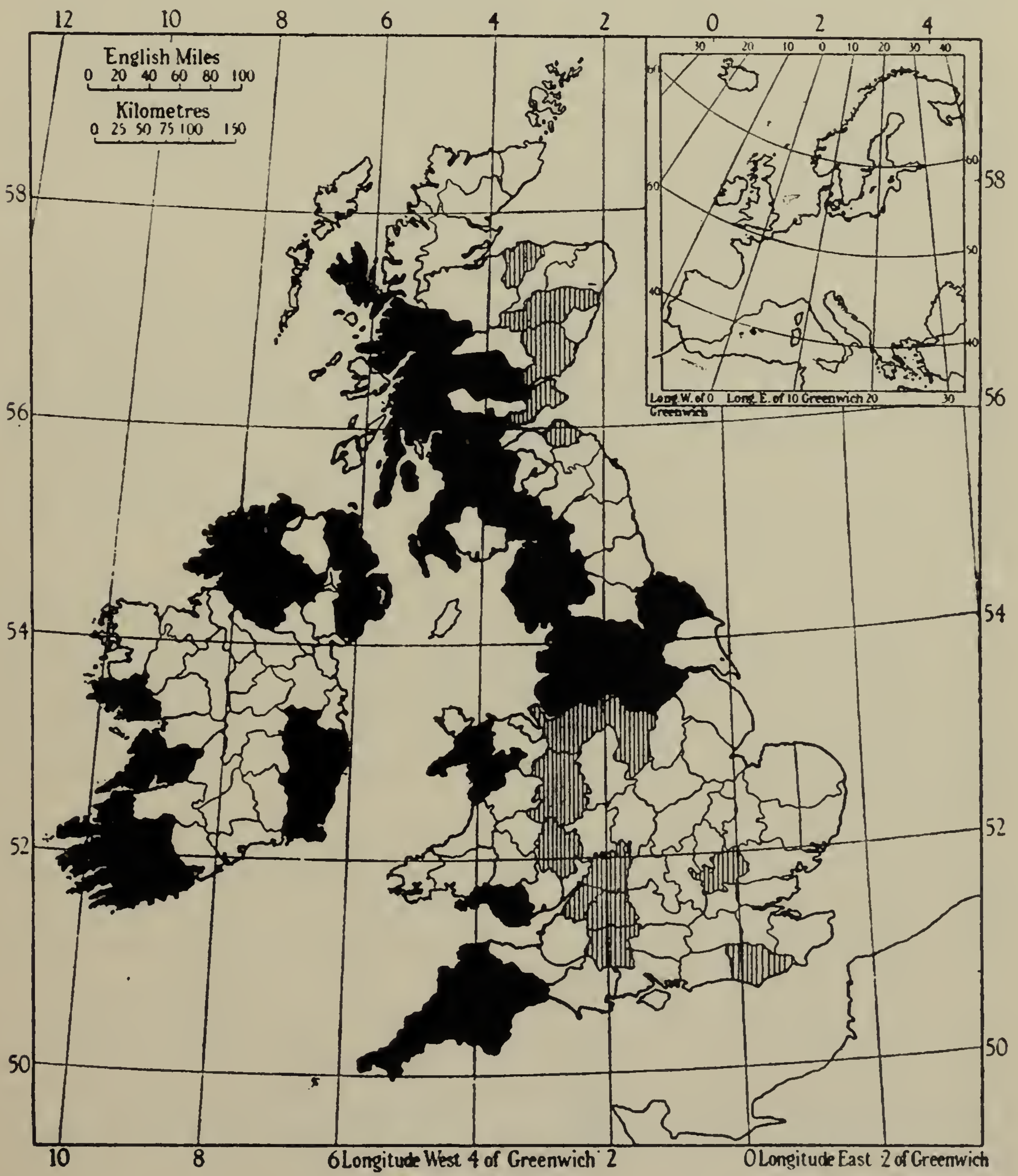

Fig. 20.

Present distribution in Great Britain of *Epilobium pedunculare* A. Cunn. In vice-counties hatched not more than two records have been traced, and some of these are not recent.

best in conditions similar to those of its coastal and alpine habitats in New Zealand. The plant is absent from the east, south-east, and midland counties of England. It appears to have been introduced into gardens either deliberately as a rock plant or accidentally with plantings of New Zealand shrubs. If unchecked, it becomes a rampant weed. The shallow fibrous rooting system requires a moist or protected substratum and, although the plant is normally perennial, it can be killed by long continued drought. Thus, for maintenance and spread, it is largely dependent upon seed. The flowers are self-pollinated and nearly all ripen seed, so that spreading is not limited by dependence on the presence of pollinating insects. The very numerous minute windborne seeds may remain suspended in air for long periods and be carried for long distances. Under laboratory and greenhouse conditions, germination of fresh seed is practically 100%, and this proportion was little diminished when using seed which had been kept dry over winter (September to February). Plants which have dried up out of doors are abundantly replaced by seedlings germinating under cover of the crowded dead leaves and stems.

E. pedunculare occurs on various types of soil in both 'acid' and limestone districts. It colonises freshly disturbed surfaces, bare ground especially when stony, gritty or sandy, or moist but porous and well drained; e.g. scree filled gullies, sandy or gravelly stream and river margins, stone and slate quarry waste (N. Wales), rubbish tips (Buxton and S. Wales), ballast heaps, railway cuttings as well as roadside situations such as walls and stony hedgerow banks. It is one of the few species colonising the china clay dumps in Cornwall.

The plant is also found well established in close association with low growing or creeping species of similar habit to itself. It is frequently recorded as growing closely intermingled with *Anagallis tenella* (L.) Murr. or associated with *Chrysosplenium oppositifolium* L., sometimes at high altitudes with the addition of *Cochlearia alpina*. It will grow in wet moss or grassy turf and in heather and sphagnum moorland.

The presence of *E. pedunculare* on roadside situations may perhaps be correlated with increase in road traffic especially lorries laden with quarried materials. Increase in the number of tourists and walkers may have helped to bring it to some of the more remote and isolated districts especially at high altitudes.

I would here record my grateful thanks to Mr. Hyde, National Museum of Wales, the late Mr. A. J. Wilmott and Mr. E. B. Bangerter, British Museum (Natural History), Dr. Ll. Praeger, the late Dr. Graham, St. Andrews University, and Dr. R. Cooper, Auckland Museum, New Zealand; also to Messrs. J. R. Lee, J. E. Lousley, N. Woodhead, and R. D. Tweed. I am also greatly indebted to the many officials and members of local scientific and naturalists' societies and others who have so generously responded to my enquiries for records, specimens and information.

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EPILOBIUM ADENOCAULON IN BRITAIN
(Exhibit)

G. M. Ash

The exhibit attempted to show the remarkable spread of a North American Willow-herb in Britain after its identification in 1932. Although herbarium specimens were found to date back to 1891, from Leicester, it does not seem to have spread from there in the same way that it has spread in the south of England since 1932.

Epilobium adenocaulon Hausskn. was first described from North America in 1879 and was first identified in Europe from Poland in 1917. Since then it has been recorded from many other countries (including France this year, 1952), being first identified in Britain from Surrey in 1932. The exhibit included a series of maps of various dates showing its gradual spread through Britain, especially in the south, until, by 1952, it had been recorded from upwards of 32 vice-counties; with more records since then. A few sheets of herbarium specimens of historic interest were shown, together with some points of difference from our other Epilobiums.

The status of *Epilobium adenocaulon* should not be confused with that of the numerous passing aliens introduced regularly and from time to time. There is no doubt that it has come to stay and that it has already changed the flora of Britain. Not only is it now the commonest willow-herb in many areas, but its great abundance where it does occur, and its exceptional variability in height (from 4 inches to 6 feet) have changed the aspect of many places. As an inoffensive garden and arable field weed, it is quite exceptional among our native willow-herbs. The question is:—Why has it made such rapid progress in recent years whilst remaining more or less static near Leicester for 50 years?

In the discussion which followed, Dr. Heslop-Harrison said he was especially interested in Mr. Ash's remarks about the enormous variation, particularly in stature, of *Epilobium adenocaulon* in Britain. He asked whether he had attempted comparative cultivation of the species from different habitats, and, if so, whether the progeny of the extremely tall and extremely dwarf forms converge to an intermediate stature when grown in the same habitat, or whether the size differential persists. Mr. Ash replied that he had not attempted comparative cultivation but the species occurred under an extraordinary range of habitat conditions.

Mr. Ash distributed copies of a duplicated clavis to the British *Epilobia* to those present at the Conference with the object of facilitating the detection of *E. adenocaulon* in additional localities. It is thought that readers will be glad to have this available in a more permanent form and it is therefore printed below.

A SUGGESTED SHORT KEY TO THE SPECIES OF EPILOBIUM TO BE FOUND IN GREAT BRITAIN.

1 a. Creeping prostrate plants with sub-orbicular leaves and erect capsules ...... *E. pedunculare* A. Cunn.
b. Small sub-glabrous alpine plants with procumbent or ascending stems; leaves acute 2
c. Plants normally one foot high or more and erect 3

2 a. Leaves narrow elliptical, mostly entire ...... *E. anagallidifolium* Lam.
b. Leaves ovate and toothed ...... *E. alsinifolium* Vill.

3 a. Flowers irregular, in long terminal leafless racemes. Petals spreading from the base ...... *E. (Chamaenerion) angustifolum* L.
b. Flowers regular, axillary or in short racemes, leafy at the base. Petals erect at the base 4

4 a. Stigma deeply 4-lobed 5
b. Stigma club-shaped 8

5 a. Flowers large, leaves distinctly clasping the stem ...... *E. hirsutum* L.
b. Flowers less than 1 cm. in diameter 6

6 a. Pubescence of the inflorescence consisting of patent glandular or eglandular hairs only; never adpressed. Lower parts of the stem generally covered with woolly hairs. Very variable ...... *E. parviflorum* Schreb.
b. Pubescence of the inflorescence consisting of numerous short patent glandular hairs with numerous crisped adpressed hairs 7

7 a. Leaves short stalked, cordate at base with bayed teeth Flowers usually red ...... *E. montanum* L.
b. Leaves lanceolate with cuneate base distinctly stalked; teeth forward directed. Flowers white in bud turning to rose colour ...... *E. lanceolatum* Seb. & Mauri

8 a. Pubescence of inflorescence predominantly of numerous adpressed hairs 9
b. Pubescence of inflorescence consisting of an equal proportion of patent glandular or eglandular hairs and adpressed ones 10

9 a. Plant wholly without glandular hairs. Leaves generally parallel sided, their limbs decurrent down the stem, teeth acute, surface uneven and shiny ...... *E. tetragonum* Curt.
b. Plant wholly without glandular hairs. Leaves lanceolate, narrowed to a short stalk, never decurrent, surface dull ...... *E. Lamyi* F. Schultz
c. Plant always with a few patent glandular hairs on the calyx-tube. Leaves very variable ...... *E. obscurum* Schreb.

10. a. Leaves elliptical, distinctly stalked with a cuneate base, teeth numerous, degree of pubescence very variable. Seed without appendage ...... *E. roseum* Schreb.
b. Leaves narrow lanceolate tapering at both ends, sessile, teeth very obscure or absent. Seed with an oblong pellucid appendage ...... *E. palustre* L.
c. Leaves oblong-lanceolate with a cordate base, teeth numerous, petiole short. Flowers small and numerous; seeds with a rounded pellucid appendage ...... *E. adenocaulon* Hausskn.

In the identification of Willow-Herbs the *quality* of the pubescence is all important; the *quantity* is unimportant, varying with the habitat.

HYBRIDS.

Hybrids occur very frequently in the genus and within limits generally exhibit characters intermediate between the two parents. The following characters may help to pick out hybrids from true species. The characters are arranged in the order most noticeable.

1. Plant larger and more branched than either parent.
2. Flowers larger than in either parent or alternatively diminutive.
3. Tips of the petals markedly deeper in colour.
4. Pods shortened and undeveloped.
5. Seeds mostly abortive
6. Leaves intermediate in shape between the parents.
7. Pubescence intermediate in character, but variable.
8. Stigmas varying on different plants from shortly club-shaped to obscurely cruciform.

It would be impracticable to draw up a key for all the numerous hybrids, but it is always a great help to know what true species were present at the site.

A CHANGING FLORA AS SHOWN IN THE STATUS OF OUR TREES AND SHRUBS

E. F. Warburg.

When I was asked to speak at this conference I was more fortunate than some of yesterday's speakers in that I was, at least partly, allowed to choose my subject. I asked to speak on alien woody plants because I felt that they had been much neglected in comparison with herbaceous ones. For example, even plants such as the casual brewer's aliens at Burton-on-Trent, which have not become permanently established, have been more intensively studied than such permanent members of our flora as *Quercus Cerris* L. and *Rhododendron ponticum* L. of which, had this conference been held two months earlier, it could have been said that they did not figure in any British Flora.

Other speakers have already told you about the natural changes that our climate and vegetation have undergone since the last glacial period and I do not propose to go into this further except to mention the importance of post-glacial research in elucidating the changing range of many species. Trees whose pollen is preserved are among the most satisfactory of these (e.g., the range of *Fagus* as a native tree has contracted considerably compared with earlier times).

Another example based on rather different evidence which will be discussed later this afternoon is *Buxus,* and I shall return to similar points later. You have already heard that for a long period in the post-glacial the greater part of this country (especially that with which I am mainly concerned in that it is there that most of our woody aliens are to be found) was fairly completely covered with forest and that man has been responsible for the present open nature of the country. This process has, of course, been responsible for enormous quantitative changes in the area occupied by different species, and the isolation of our woodlands must prevent to a large extent the spread of many species by natural means. There is, however, no evidence that man has been responsible for the extinction of any woody species. As an example of an indirect effect of this process one may perhaps quote the two species of *Crataegus* which Mr. A. D. Bradshaw has studied, and on which he will have something to say presently.

Man has worked also in another way in introducing alien trees and shrubs, as follows: —

1. *Forestry.*

Trees planted on a large scale for forestry are our native hardwoods, the sweet chestnut (*Castanea sativa* Mill.) and perhaps the sycamore (*Acer Pseudo-platanus* L.), a number of exotic conifers and our native *Pinus sylvestris* L. On the whole, these exotic

conifers, although they are now a permanent feature of our landscape, have not become extensively naturalised. The European larch (*Larix decidua* Mill.) has probably been the most successful. Some of the western North American species have, however, been here only a comparatively short time and may yet spread, thus *Pseudotsuga taxifolia* (Poir.) Britt., the earliest of them, was introduced in 1827, and *Thuja plicata* Lamb. in 1853. Coniferous plantations do, however, contribute extensively to "The Changing Flora of Britain" by killing out the ground vegetation below them and must be ranked with the military, hydro-electric schemes, and building operations as the most important factors in the reduction of many native species. Of our native hardwoods, the beech may again be used as an example. Its native range to-day probably extends from south-east England to Hertfordshire, Gloucestershire, Brecon, Glamorgan, Somerset and Dorset although it is planted extensively almost throughout the British Isles and regenerates freely in Aberdeenshire.

2. *Ornament.*

It is probably among species which have been planted primarily for ornament that one must look for the greatest influx of woody aliens into our flora—a few examples which will not be discussed further are:—*Amelanchier laevis* Wieg. (extensively naturalised, for example, amongst native vegetation in the Hurtwood, Surrey), *Cotoneaster Simonsii* Baker, *Sorbus intermedia* (Ehrh.) Pers.

3. *Fruit.*

Fruit trees and shrubs present a special problem. Many have been cultivated for long periods (it would be interesting to know what light fossil evidence throws on the subject). Some are undoubtedly native in this country although the wild form is not always the same (e.g., apple, sweet cherry). Others (e.g., pear, medlar) are almost certainly introduced; neither of these ever looks native as far as I know and the same is, in my experience, true of *Prunus domestica* L. which is probably not wild anywhere, though its subspecies *insititia* (L.) Poiret is often considered native. This subspecies seems to be a decreasing tree, perhaps owing to its being grown less than formerly, and the same is probably true of the sour Cherry (*P. Cerasus* L.). There appear to be no recently introduced fruit trees.

4. *Other purposes.*

These can be taken as including:—

(a) *Hedges. Prunus cerasifera* Ehrh. is an example. (The hedges of this in full flower are a feature of the countryside in spring, especially in East Anglia.) I have not seen it as a self-sown plant and know no reliable record of it as such; it fruits rarely and rather sparingly in this country. *Fuchsia magellanica* Lam. may also be quoted.

(b) *Cover and food for game.* Examples are *Gaultheria Shallon* Pursh and *Mahonia Aquifolium* (Pursh) Nutt. and perhaps also *Rhododendron ponticum.*

(c) *Reclamation of unfavourable soils and shelter belts.* Examples are *Acer Pseudo-platanus* L., *Alnus incana* (L.) Moench, *Pinus nigra* Arnold subsp. *nigra* and *P. mugo* Turra.

Unlike other types of alien discussed during this conference, accidentally introduced woody plants are probably unimportant and I can think of no example that has become established. (It is true that *Phoenix dactylifera* L.—the Date Palm—figures in Druce (1928) but it need not be considered seriously.)

I would now like to discuss a few individual species.

Acer Pseudo-platanus L. (the Sycamore) is one of the longest naturalised trees introduced in historic times. It has been studied by Jones (1945) and the following account is taken from his paper. He shows that it was fairly certainly introduced to Scotland (Perthshire) in the 15th or at least the early 16th century. The first definite evidence for England is Lyte (1578) in *Niewe Herball* —"there is here and there a tree of it planted in England", whereas Turner (1562) does not mention it as in England though he mentions it as occurring in Germany. A hundred years later, Evelyn (1662) suggests it is only suitable for "distant walks" on the grounds of its "Honey-dew leaves". It had presumably become more common. Dr. Jones believes, however, that it did not become widely used in shelter belts, plantations, etc., until the end of the 18th century, the first flora to give "woods" as its habitat being Abbot's of Bedfordshire (1798) and the first definite evidence of natural regeneration by Samuel Hayes (1794) in Co. Dublin. Since that time it has been extensively planted and now doubtless occurs in every vice-county in the British Isles, though there were nine for which Dr. Jones was unable to trace records. It is now, of course, frequent everywhere and occurs and fruits up to at least 1,600 ft. (in Shropshire).

Cotoneaster microphylla Lindl. This Himalayan species was introduced into this country in 1824 (Bean, 1925) though the first definite record as a naturalised plant appears to be 1890, according to Druce (1932). It became "respectable" (a term the meaning of which will become clear later) apparently at a fairly early date. Localities where it occurs naturalised are usually given in detail in County Floras. Twelve southern and central English County Floras were chosen as being fairly comprehensive in their inclusion of aliens and reasonably modern—all having been published since 1895. These were:—Cornwall (Davey, 1909) with supplement (Thurston & Vigurs, 1922); Devon (Martin & Fraser, 1939); Somerset (Murray, 1896) with supplement (Marshall, 1914); Hampshire (Townsend, 1904) with supplement (Rayner, 1929); Sussex (Wolley-Dod, 1937); Kent (Hanbury &

Marshall, 1899); Surrey (Salmon, 1931); Berkshire (Druce, 1897); Oxfordshire (Druce, 1927); Buckinghamshire (Druce, 1926); Gloucestershire (Riddelsdell, Hedley & Price, 1948); and Leicestershire (Horwood & Noel, 1933). Out of these, *Cotoneaster microphylla* is mentioned in six and in each of these, except Cornwall, its known localities are given in detail. There are 20 British specimens in the Oxford University Herbarium, which includes Druce's. Its characteristic habitats in this country are rocky limestone pastures, limestone cliffs and, in contrast to the sycamore, it seems to be little planted outside gardens and must owe most of its spread to birds.

Its recorded range by vice-counties is 1-4, 6, 9, 10, 13-15, 17, 33, 34, 38, 39, 41-45, 47, 50, 52, 56, 62, 65, 67, 69, 70, 80, 88-90, 103, 104. It would probably be fairly easy to map its known stations. It may be noted that it finds a place in both Druce (1932) and Butcher & Strudwick (1930).

Rhododendron ponticum is chosen as a contrast to the last species. It is probably much commoner as a naturalised plant and is of much greater ecological importance. For example, in the Killarney oak woods it is replacing holly as the shrub layer over extensive areas and becoming a menace to the native vegetation. All of you have doubtless observed the same sort of thing happening elsewhere. Its date of introduction was 1763, but it is not 'respectable' and I have not been able to trace its first record as a naturalised plant. Of the 12 county floras quoted it is only mentioned in one (Sussex) and there somewhat apologetically— "Though not usually recorded in county floras, the Rhododendron is as completely naturalised as *Pinus sylvestris, Acer Pseudoplatanus, Castanea sativa* and other planted trees. It occurs wherever it has been planted and reproduces itself freely from seed". The flora of Surrey mentions the much rarer aliens *Gaultheria Shallon* and *Kalmia polifolia* Wangenh., but does not mention *Rhododendron*. There are only five British specimens in Herb. Oxford. It is likely that the available data would be quite inadequate to give any picture of either its present-day range or its spread.

Quercus Cerris L. is another extensively naturalised plant which occupies in "respectability" an intermediate position between the two preceding; nine of the 12 county floras give it, but mostly without localities and some dismiss it as "planted". Davey (1909) gives it as "perfectly naturalised in many parts" and this is probably true of most of the counties though Wolley-Dod (Sussex) says "very rare" and gives localities; three others give localities also but they are manifestly inadequate. There are 12 British specimens in Herb. Oxford. It is not in Druce (1932) nor in Butcher & Strudwick (1930). It was introduced in 1735.

Buddleja Davidii Franch. This plant, which was introduced about 1890, is in a rather different category from the examples already given. Though occasionally recorded from woods and

more frequently from railway banks before the last war, its main chance came during the war and it is now common on bombed sites in many places. How far it will persist as a naturalised plant remains to be seen.

Before leaving the subject of undoubted aliens a few general points may be made.

(1) There has been great un-evenness of treatment of woody aliens, which applies also to other aliens in some measure. Some have been regarded as "respectable", others are not.

(2) Where such aliens are mentioned, the presence or absence of natural regeneration and its extent are often not mentioned. Contrast, for example, the bare statement 'plantations' for *Q. Cerris* in *Fl. Bucks.* with the statement under *Amelanchier laevis* (as *canadensis*) in *Fl. Surrey*—"naturalised over several square miles in the Hurtwood"—but even this gives no real idea of the plant's abundance and this Flora does not mention *Rhododendron*!

I would like at this point to put in a plea that more study should be given to woody aliens of all kinds and that where specimens are preserved they should be accompanied by full data of the occurrence and amount of regeneration.

(3) It would be interesting to know what factors have caused the success of certain plants rather than of their relatives. Why is *Rhododendron ponticum* the only member of that genus to have spread extensively? A possibility is that it is the only one much planted outside gardens and that it is also used as a stock for grafting. Why has *Cotoneaster microphylla* spread freely and not *C. frigida* Lindl., which was introduced at the same time, is very widely grown, and fruits abundantly? Why are there no naturalised *Berberis* except *B. vulgaris*? Much clearly depends on the extent of planting.

(4) Is the large amount of planting along the new roads at the present time of many exotic shrubs going to have an effect? I hope careful records are being kept.

I now want to turn to a more difficult and in some ways more important subject—that of ascertaining the native range or status of certain plants. It has been touched on earlier. The status of many of our trees is in question, thus *Populus nigra* L. and *P. canescens* Sm. may or may not be native trees. I want to take as an example *Sorbus Aria* (L.) Crantz. This is an unquestionably native tree but it has been extensively planted, since it is very ornamental. Its range by vice-counties, according to Druce (1932), adding to this such additions as have been made since, is shown in the accompanying map (Fig. 22). It will be seen that this range extends over the greater part of the British Isles. Its true range as a native plant, as far as I have been able to ascertain it, is shown on Fig. 21. *S. Aria* is thus confined to a ± continuous area in the south-east of the country. This fits in with its

Fig. 21.
Probable native vice-comital distribution of *Sorbus Aria*.

Fig. 22.
Native vice-comital distribution of *Sorbus Aria* according to Druce's *Comital Flora*.

European range; it is a Continental species. It also occurs, apparently native, in Galway. In this it agrees with certain other calcicole species which occur mainly in the east of Great Britain but which also occur in isolated localities in Ireland (e.g., *Viola stagnina* Kit., *Helianthemum Chamaecistus* Mill., *Astragalus danicus* Retz., etc.). This, however, is not relevant to this paper.

The reason for the discrepancy is two-fold: —

(a) Confusion between *S. Aria* and allied species. This is responsible for many of the records from W. & N. England, some Scottish and many Irish records.

(b) Records of naturalised or even planted trees which have not been separated from native ones. This is responsible for all the records from E. England, most of the Scottish ones and many of those from elsewhere. It has probably been more important than (a).

The evidence for the native range is mainly based on personal field observations supplemented by county Floras. The latter, if properly used, are a great help in this type of work. One can get from them a good idea of the habitats and occurrences of the plant in the county in question. The actual statements in them, however, of the status of the plant are of less value and must be carefully sifted, being often based on preconceived ideas.

Two types of evidence, valuable in other cases, seem to be of little use here. Herbarium specimens are usually unaccompanied by details of status and regeneration and are thus only of value in sorting out the records of non-native *S. Aria* from native stations of other species. As far as I know there are no fossil records for *S. Aria* and, even if it were found fossil, it would be unlikely that its remains would be separable from those of related species. The same applies to philological evidence.

Another vexed and now probably insoluble problem, is presented by *Pinus sylvestris*. It is universally acknowledged to be native in Scotland and the woods in such areas as the Spey Valley and Glen Affric certainly represent the remains of the old Caledonian Forest. The Scottish plant, also, is a separate geographical race. Until recently *P. sylvestris* was almost universally believed to be introduced in England. In recent years fossil (pine pollen occurs throughout post-glacial deposits) and other evidence suggests that the pine may have persisted in England and that relicts may exist. Dr. A. S. Watt and I, in some work done during the war, reached the conclusion, based partly on the form of the trees and partly on other evidence, such as the presence of *Goodyera repens* (L.) Br., that certain Norfolk pines may well be such relics. It is possible that a combined study of the plants *in situ,* of fossil evidence and a comparison of the morphological features of British plants with known foreign races, and perhaps also philological and historical evidence, might enable definite conclusions to be drawn.

There are in this country a limited number of woody plants which are never planted and perhaps these may be useful pointers.

I may perhaps again consider *Sorbus*. Apart from *S. Aria, S. Aucuparia* L., their hybrid, and perhaps *S. torminalis* (L.) Crantz, our native species do not seem to have been planted. Most of them are to-day plants of limestone cliffs but are heavily grazed by sheep when they can reach them and they may have formerly extended to other habitats as, in fact, *S. hibernica* E. F. Warburg still does. They may be put into two main groups (1) comparatively widespread, (2) local endemics.

The most widespread of them is *S. rupicola* (Syme) Hedl. and it is the only one which occurs in an apparently identical form on

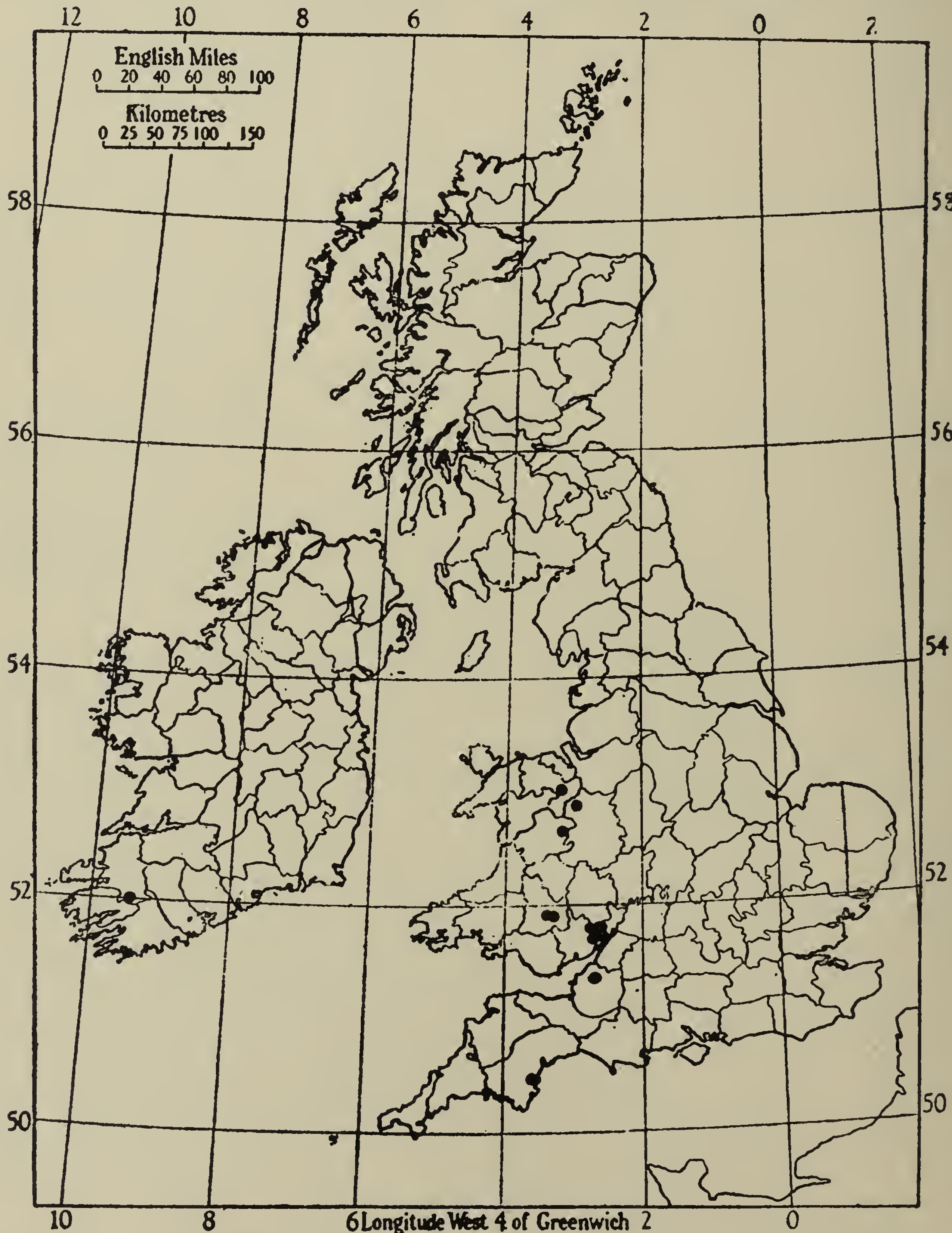

Fig. 23.
The distribution of *Sorbus anglica*.

the Continent, where it occurs in Scandinavia. It has a number of isolated localities in W. & N. England, Wales, Scotland, and N. & W. Ireland.

Another example is *Sorbus anglica* Hedl. which is known from the Wye Valley, where there are several stations, and from seven other localities in S.W. England, Wales and Kerry (see fig. 23). Though endemic, it has near allies on the Continent:—*S. Mougeotii* Soy.-Willem. & Godr. from the W. Alps; *S. austriaca* (Beck) Hedl. from the E. Alps, and *S. subsimilis* Hedl. from Norway. This may perhaps be an example of a species more widespread in the post-glacial that had become fragmented and differentiated. Minor differences exist in the British forms also. It may be compared with *Veronica spicata* L. subsp. *hybrida* (L.) E. F. Warburg and *Helianthemum canum* (L.) Baumg., already referred to by other speakers. It should, however, be mentioned that this group of *Sorbus* is probably apomictic.

Narrow endemics include *S. minima* (Ley) Hedl., confined to limestone cliffs near Crickhowell (Brecon) and *S. bristoliensis* Wilmott of the Avon Gorge. Both these are triploid and apomictic and perhaps originated by hybridisation not far from where they exist to-day. It is remarkable that they have not been spread further by birds, particularly in the light of the spread of such plants as *Cotoneaster microphylla* referred to earlier.

Ulmus is another woody genus in which endemics occur, though they have been more extensively planted.

I think that studies of such endemic species taken in conjunction with studies of woody aliens may help towards an understanding of the large and difficult group of man-assisted species.

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Dr. Melville then spoke on "Some Historical Factors in the Distribution of British Elms" as follows:—Historical factors have played an important part in the distribution of the British elms. Some species, among which are *Ulmus procera* Salisb. and *U. cornubiensis* Weston (*U. stricta* Lindl.) appear to have colonised our land from the south. In glacial times the English Channel and the continental shelf, now occupied by the Bay of Biscay, were dry land, owing to the general lowering of the sea level by about 300 feet and an isostatic rise in the earth's surface in this area. Here the climate would have been suitable for the survival of elms, and on the passing of the glacial epoch and gradual flooding of the continental shelf, the elms could migrate northwards and colonise southern England.

The remaining British species or their progenitors probably migrated westward from the Continent across the North Sea area before it became flooded. The Wych Elm, *U. glabra* Huds., being the hardiest, probably came first and in due course extended its range throughout Great Britain. The remaining species, including *U. Plotii* Druce, *U. coritana* Melville and *U. carpinifolia* Gled., were probably later arrivals. They spread out over East Anglia and the Midlands and a mixed population of hybrids must have developed at an early date. All the species inhabiting this part of the country are interfertile and hybridise freely, with the exception of *U. procera*, which flowers before the other species and usually has its fruits destroyed by cold.

The resultant hybrid swarms are still with us, but other historical factors have played a part in determining their present composition and distribution. We now find in East Anglia, especially in Essex and the adjacent part of Hertfordshire, that each valley contains its own hybrid form. On passing over the ridge into the next valley a different hybrid form is encountered, and so on with the next one. In some of the larger valleys the elm population changes as one proceeds down the valley, although the forms occurring in one valley are generally closely related to one another. It is evident that this diversification must have arisen since the Ice Age, since at the time of the last glaciation conditions were unsuitable for the growth of elms in central and eastern England. The elm is a moisture-loving tree favouring the valley bottoms. This would lead to partial isolation of the valley elm populations even when this part of the country was completely forested, as it doubtless was in Neolithic times. At a later stage man played a part in making the isolation more complete. It was easier for early man to clear the drier hill tops than the ranker growth in the valleys. Once this had been achieved, the valley elm populations were virtually isolated, since in these wind pollinated trees the concentration of pollen from the local population would have been far higher than that brought by air currents from neighbouring valleys. In spite of the clearing of the remaining forests from the valley bottoms at still later dates, the elm populations have remained essentially natural. Their propensity for producing suckers has enabled them to survive in hedgerows.

HUMAN INFLUENCE ON HYBRIDISATION IN CRATAEGUS (Exhibit)

A. D. Bradshaw.

The taxonomy of *Crataegus* in Britain is difficult. It has been recognised that this is because *C. monogyna* and *C. oxyacanthoides* hybridise and give rise to intermediate forms.

C. monogyna Jacq. is common in open scrub and hedgerows on a wide variety of soils, from heavy clays to dry chalks. *C. oxyacanthoides* Thuill. is restricted to the heavy clay soils of the Midlands and S.E. England. Various characters, such as capacity for flowering in dense shade, spreading growth-habit and well arranged leaf mosaic suggest that it is primarily adapted to woodland environments. *C. monogyna* seems unable to tolerate the extreme woodland environment in which *C. oxyacanthoides* is found. It is, for instance, unable to produce any flowers at all in dense shade.

The evidence for hybridisation is not direct, since so far no artificially produced hybrids have been grown to maturity. But in undisturbed woodlands it is possible to find pure populations of *C. oxyacanthoides,* and, in open scrub, pure populations of *C. monogyna.* Whenever two such populations are in contact, the intermediate forms occur as a zone between them, suggesting their origin by hybridisation. Although there is a difference in their flowering times, there is ample opportunity for intercrossing between the two species. A large number of artificial crosses has shown that fertile seed is set as easily in crosses made between the two species as in crosses made within the species.

It appears that under original undisturbed woodland conditions the two species were ecologically isolated, neither being able to tolerate the proper habitat of the other. But the effect of man's destruction of woodlands has been to destroy this isolation. By making clearings in woodland he has made areas which *C. monogyna* has been able to invade, and which has brought it in close contact with the woodland *C. oxyacanthoides.* By selective felling and undergrowth clearance, he has reduced the density of the woodland sufficiently to allow *C. monogyna* to invade the woodland itself. As a result, populations with large numbers of hybrids have been developed in disturbed woodlands. This is a similar situation to that in *Melandrium* (Baker, 1948).

The amount and nature of man's disturbance of woodland has varied. Thus, by examination of different woodlands, it has been possible to find populations with different degrees of hybridisation. For comparison of such populations, individual plants were measured for one character only, that of the degree of indentation of the leaves. This has always been held to be an extremely

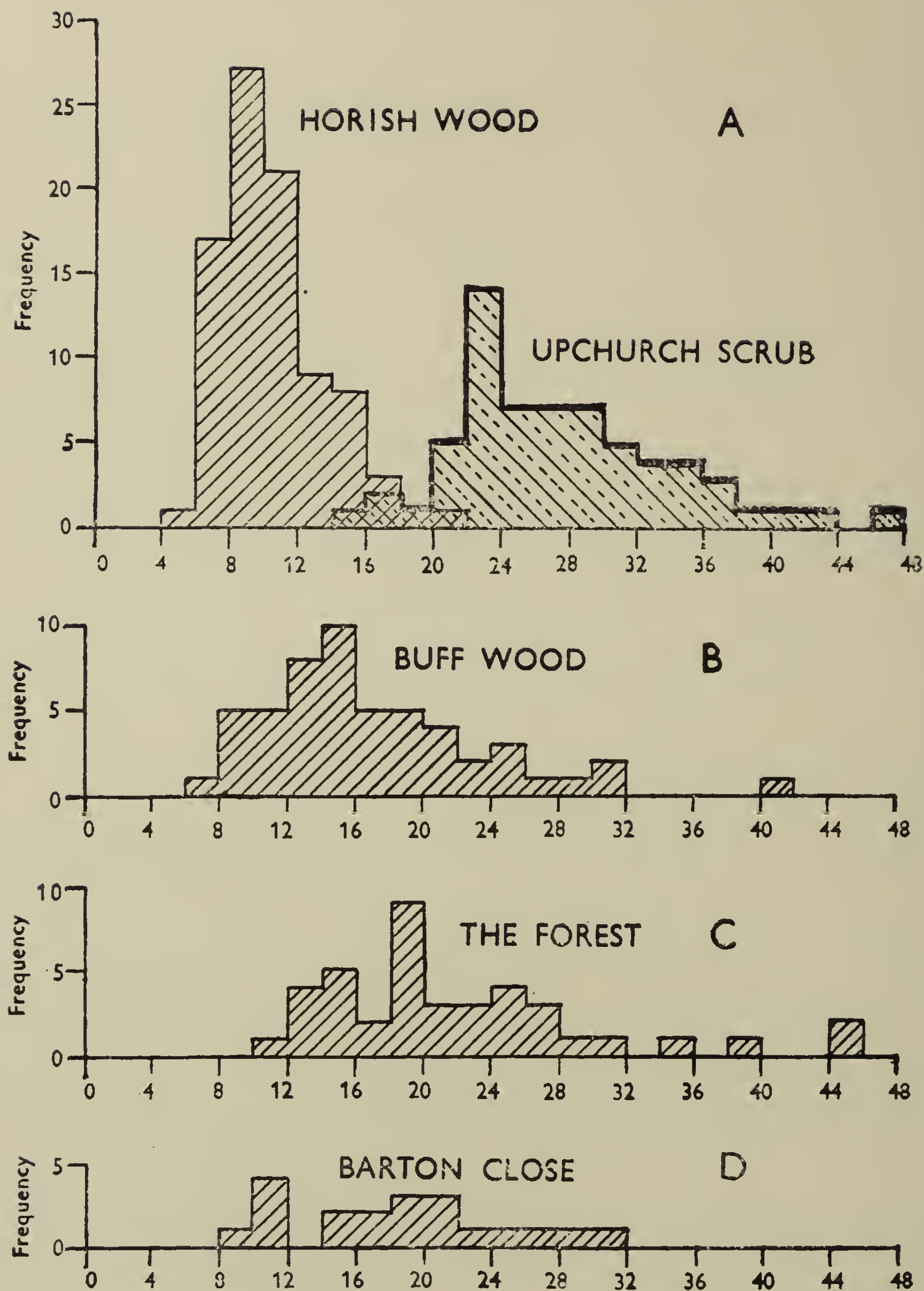

Fig. 24.

Degree of Leaf Indentation in Populations of *Crataegus*.

A. Horish Wood, Maidstone, Kent. On Gault clay. Carefully managed dense hazel coppice with oak standards. Pure *C. oxyacanthoides*.
Upchurch, Rainham, Kent. In disused chalk pit. Open scrub with roses, etc. Pure *C. monogyna*.

B. Buff Wood, W. Cambs. On heavy boulder clay. Badly managed mixture of oaks and hawthorn and hazel scrub. *C. oxyacanthoides*, many hybrids, and some *C. monogyna*.

C. The Forest, Ashford, Kent. On Weald clay. Badly managed very open oak wood with scattered hawthorns and much open ground. Few *C. oxyacanthoides*, many hybrids, and *C. monogyna*.

D. Barton Close, Cambridge. On heavy boulder clay. Old hedge in town. Traces of *C. oxyacanthoides*, but mostly hybrids.

good diagnostic character for the two species and is closely correlated with other diagnostic characters such as seed number, flowering time, growth habit, flower shape. It is not affected by the environment to any extent. The population values have been made into frequency distribution diagrams.

Pure *C. oxyacanthoides* populations give a diagram shape such as that of Horish Wood, pure *C. monogyna* populations that of Upchurch (fig. 24a).

Woodlands on the Gault clay belt of the North Downs that have been carefully managed as coppice and standards for a considerable period, such as Horish (fig. 24a), Longham and others also near Maidstone, Kent, maintain an almost pure population of *C. oxyacanthoides.* A similar situation is found in the middle of Buff Wood in W. Cambs., on heavy boulder clay, which has been maintained as dense high forest with only a little coppice.

In woods that have been considerably disturbed such as the northern end of Buff Wood (fig. 24b) which is a confused mixture of hawthorn scrub and scattered oaks, and The Forest near Ashford, Kent, (fig. 24c) which is an open wood with few standard oaks and much open ground, there has been ample opportunity for intermixing of the two species and this has resulted in populations consisting largely of hybrids.

The population from Upchurch near Rainham, Kent (fig. 24a) is an example of a normal *C. monogyna* population outside the normal distribution of *C. oxyacanthoides,* and therefore quite pure.

It is possible to find small populations of hawthorns in built-up areas in town, relics of former natural populations. These are usually of *C. monogyna.* But the population of Barton Close, Cambridge (fig. 24d) has an element tending towards *C. oxyacanthoides.* The bushes are part of an old hedge whose origin was probably from cuttings from the hybrid scrub plants found on the edges of the woods on the heavy clay to the west of the town. Many such hedges are to be found north of London.

A similar population was found in Winnington Road, Highgate, London, N.2, consisting of scattered bushes in various private gardens. The older Ordnance Survey maps show that these are on the site of the old Bishop's Wood now no longer in existence. This wood presumably had a good *C. oxyacanthoides* population, in common with other similar woods on London Clay.

When forest cover was continuous it seems that *C. oxyacanthoides* was very common on heavy clay soils. With the destruction of woodland not only causing the loss of suitable habitats for it, but also allowing the introgressive hybridisation with *C. monogyna,* pure populations of *C. oxyacanthoides* are becoming increasingly uncommon. There is little doubt that this process will continue.

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IS THE BOX-TREE A NATIVE OF ENGLAND? (Exhibit)

C. D. PIGOTT AND S. M. WALTERS.

The native status of Box (*Buxus sempervirens* L.) in this country has often been questioned, and although most authorities have been inclined to accept it as native in a few famous localities such as Box Hill, the doubt persists in the literature. Thus Elwes and Henry (1913) wrote:—"Whether Box is native of England or not is doubtful; but it is certainly naturalised, if not truly indigenous, in a few localities . . . ." And Tansley (1939) wrote:—"occurs apparently wild on chalk and oolite of the south of England. Doubt has often been thrown on its nativity; it is absent from the north of France except where it has been planted; and since its wood is valuable, it is one of the plants that may have been introduced by the Romans".

Two main arguments seem to underlie the doubt: firstly, that, because the word 'box' is a loan-word from the Latin *"buxus"*, the plant was introduced by the Romans (cf. Charlesworth (1949)); and, secondly, that 'Box is absent from the north of France except where planted'. Let us consider these in turn:—

1. *Evidence from the name.*

Although some 19th century philologists (e.g. Hehn (1870)) developed the argument that where a loan-word exists in a modern language, the object concerned had been introduced by the people from whose language the word had been borrowed, later authorities (e.g. Schrader, in Hehn, ed. 6 (1894)) pointed out that, although this might be true in certain cases, it is by no means necessarily so, and can indeed often be demonstrably false. Schrader emphasises instead, that a new use or significance introduced by the invading culture may suffice to plant a loan-word into the language for an object (plant, animal, etc.) already known to the native population. The Latin "*buxus*" is itself generally considered to be a loan-word from the Greek (πυξος); and this is readily understandable in view of the fact that there was a flourishing Greek trade in box-wood in the Eastern Mediterranean and the Black Sea centuries before Christ. In most European languages the word is obviously a derivative of this Graeco-Latin word; and whatever its precise history, it seems clear that its presence in English, French, German and elsewhere can tell us nothing directly about the origin of the Box-tree. The absence of any trace of a pre-Roman (Celtic) word for the plant in Britain or France is worthy of comment; but the explanation may well be that any pre-Roman word was already of the "*buxus*" type and was simply submerged by the Latin form. (There *are* actually

traces of a very ancient pre-Indo-European word for the Box-tree in the Basque "*ezpel*" and a similar root in certain Southern French dialects and place-names; but the subject is highly obscure!) It is certainly not possible to believe that primitive peoples in Britain and France had no word for the plant; for there is abundant evidence that Box foliage, like that of other evergreens, has since the birth of civilisation in Europe been associated with religious rites, and particularly with burials—indeed the Christian Church has taken over this significance, as in the use of Box as an Easter "palm" in France, Belgium, and parts of Eastern Europe to-day (cf. the Romano-British burials with Box twigs).

2. *Distribution and Status of Box.*

Tansley's statement about Box in N. France seems to be traceable, via Elwes and Henry, to a short paper by Chatin (1861), in which he discusses plants in northern France associated with gardens, châteaux, etc., to most of which he assigns a Roman introduction. Box is only mentioned casually, with a guess that the "introduction" of the plant dates principally from medieval rather than Roman times; in evidence he gives a short list of localities in the Paris region, in many of which there is a medieval château or monastery. The correlation appears to be there; but

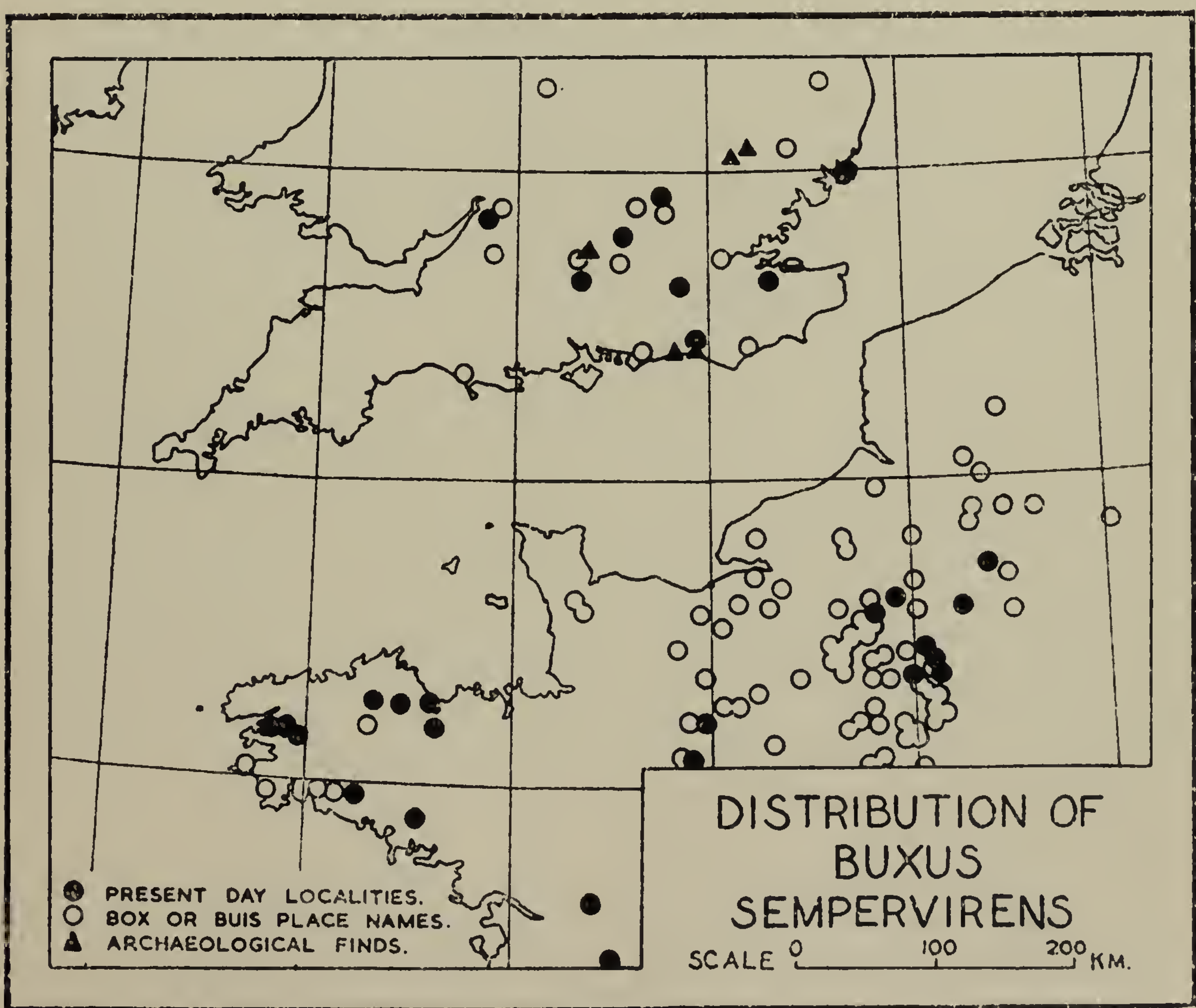

Fig. 25.

a likelier explanation than the one of medieval introduction is that those who built castles in the Middle Ages tended to choose the edges of cliffs or steep slopes, the most striking of which in the Paris area occur where the Seine erodes hard chalk (as at Les Andelys, or La Roche-Guyon)—precisely the localities where native Box might be expected! There seems really little doubt that in the Paris area, as in the Ardennes to the east and south Normandy in the west, there is native Box in very similar situations to its classical British localities (cf. Lemée, 1935); and indeed several French local floras have treated the plant as native in such places. The absence of Box from the Pas de Calais and most of Normandy may well be due firstly to the absence of suitable steep chalk slopes or cliffs, and secondly to the intensive cultivation of the chalk areas. The general distribution of Box at its N.W. limit in Europe is in fact very closely paralleled by several other sub-Mediterranean species (as was pointed out by Engler in Schrader 1894).

History of Box in France and England.

Neolithic charcoal referable with reasonable certainty to Box has been recorded from Whitehawk Camp, near Brighton, and Iron Age charcoal probably of Box from Cissbury Camp, near Worthing. In addition there are several records of Box foliage in Romano-British burials on the chalk in Cambridgeshire and Berkshire. The plant was well known in Anglo-Saxon times; records of the Box tree and particularly of place-names with Box in them are found from the 8th century onwards. The evidence for the antiquity of certain present-day localities for Box is quite impressive; even that on Sidon Hill, near Highclere, Hants, which Bromfield (1849) said was "an evident, and indeed acknowledged introduction", can be shown to have been represented by at least one Box-tree in A.D.934! (Kemble, 1849). The majority of English and French place-names derived from the word for "box" are 12th to 14th century in origin; and although it is true that, particularly in France, Box-groves were planted for their valuable wood, nevertheless the distribution of these place-names fits so well the areas where (in England) ancient Box records are available and where the most likely native habitats persist, that one feels the planting has supplemented rather than radically altered an earlier distribution. It is interesting that Dauzat (1939), studying the evidence of pre-history afforded by place-names in the region south of Chartres known as "La Beauce" comments on the 'box' place-names which are not infrequent there, but because of the rarity or absence of Box to-day in the region, he thinks the names cannot apply to Box. His general thesis, however, is that all the evidence from different studies points to an early historical period of forest and clearing with relatively little cultivation, and he points out that place-names based on other trees are frequent. It would seem that, not only in La Beauce

PLATE V.

Photo by J. E. Lousley.

Interior of the Box wood on the steep slope above the River Mole, Box Hill, Surrey.

but also throughout the range of Box in France and England, the Neolithic and subsequent forest clearings gave to the plant, as to many others, a very considerable chance of spread, particularly in scrub vegetation on chalk, and that, by Roman times, the plant might well have achieved considerable abundance (cf. the Romano-British Box in graves). Later a developing use of the wood of the tree might well have led to its cutting out, and then to its artificial planting.

When in such a picture do we assume that Box entered Britain? There is a (not certain) record for its pollen from a British interglacial deposit (on the Continent there are several interglacial finds); but we have no post-glacial sub-fossil record. We can therefore only guess; but a limited entry in the Boreal period, with a very restricted survival through the Atlantic forest maximum, would seem to be a reasonable guess. The dry Sub-boreal, with the Neolithic forest clearance, would then give the plant the chance of a secondary spread, which was probably very considerable. On such a hypothesis there would be three types of present-day Box locality:—

1. "Native" localities where the plant might have persisted since the Boreal; the steep chalk slopes of Box Hill are a good example. Here the rounded downs are interrupted by the gap cut by the river Mole and above Burford Bridge the river is actively undercutting the chalk escarpment (Plate V). It is suggested that the occurrence of *Buxus* in this locality is related to the topographical features, which have prevented the establishment of closed forest, and allowed the *Buxus-Taxus* wood to survive the 'Forest Maximum'. Although the young bushes of *Buxus* can grow n deep shade, examination of the wood suggests that only vigorous bushes in more open parts can produce viable seeds. The unstable nature of the chalk substratum is demonstrated by the accumulation of banks of chalk rubble on the upper side of the bushes and the exposure of the roots on the downhill side.

2. Survival of "scrub" localities of Neolithic or post-Neolithic origin; could not Box on ancient trackways such as Fleam and Devil's Dyke date back to this period?

3. Box planted in historic time; possibly associated with Roman villas, medieval Box groves for wood, more recent planting in shrubberies.

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THE CONSERVATION OF BRITISH VEGETATION AND SPECIES

Sir Arthur Tansley
(Chairman of the Nature Conservancy, 1949-53).

During this Conference we have heard a great deal about the various factors that have contributed, and are contributing, to changes in our flora. For my part, I have been asked to talk about the means of conserving what can still be prevented from disappearing altogether. For though we cannot stop, or even check, the continuous introduction of fresh aliens (and I imagine that most botanists would not wish to if they could), we shall all agree, I think, in wanting to preserve as much of the native flora as we can. At this Conference, I am deliberately omitting reference to the conservation of animal life, though much of the Nature Conservancy's work is devoted to that, particularly of birds and insects.

The motives of this desire are twofold. First there is the sentiment attaching to things (or most of them) which are native to Britain, intensified by a keen appreciation of the beauty and interest of many of them. We want to keep our old buildings when they are good-looking or specially characteristic of a creative age. And we do not like to see our natural landscapes, such of them as still remain, destroyed or defaced—nor our man-made rural landscapes either, with their arable and pasture, coppice and hedgerow. The second motive is scientific interest in flora and vegetation, a motive which is specific to botanists and ecologists.

With this second motive the Nature Conservancy is specially concerned, largely owing to the keenness and drive of its first Director-General, Cyril Diver, who stressed the scientific and practical importance of preserving as much as possible of the native flora and fauna and thus "cashed in", as it were, on the current high prestige of science to persuade the Scientific Advisory Council to the Cabinet, and through them the late Government, to set up the Conservancy. Nevertheless, as I have often said and written, I personally find it hard to separate the two motives within my own mind—love of the British landscapes and their plant covering on the one hand, and, on the other, interest in studying them and finding out more about them: each of these motives, in my own experience, reinforces the other.

Besides innumerable local bodies, and setting aside for the moment the National Trust, we now have four organisations of national scope concerned in conservation; two voluntary and two which are minor Government departments. The Society for the Promotion of Nature Reserves, founded by Charles Rothschild, has been at work for a good many years now, owns several

reserves and has assisted several others. The Council for the Preservation of Rural England, as its name implies, has different and wider aims. Together with its sister body, the Council for the Preservation of Rural Wales, it works largely through propaganda and by calling public attention to the most various threats to the beauty of the countryside. Under many difficulties and without any state assistance, it has done, and is doing, yeoman work on these lines. Of the two Government bodies, the National Parks Commission was set up under the National Parks and Access to the Countryside Act of 1949. It is responsible for the designation of National Parks, which are tracts of largely wild country primarily intended for the enjoyment of the public. The Commission was placed under the Ministry of Town and Country Planning, now renamed the Ministry of Housing and Local Government (a significant change of title). It was this Ministry that set up in 1945 the National Parks Committee, under the chairmanship of Sir Arthur Hobhouse, and the adjunct Wild Life Conservation Special Committee, on whose reports the Act which established the National Parks Commission was based. Unfortunately, as many people think, the Commission has little executive authority, as it was originally intended they should have. The actual management of the National Parks will rest with Local Planning Boards appointed mainly by local authorities, the National Commission acting as an advisory body to the Local Planning Boards, which must consult it, and to which it can make recommendations, but on which it cannot enforce its views.

Both the C.P.R.E. and the N.P.C. are commonly referred to as "amenity bodies", or (privately) by the often somewhat hard-faced "practical man" as "those amenity people".

Finally there is the Nature Conservancy, established early in 1949 by Royal Charter and given statutory duties and powers in the same Act as that which created the National Parks Commission at the end of that year. The Conservancy works under the aegis of the Committee of the Privy Council which also sponsors the Agricultural Research Council. But the Conservancy is directly responsible to the Lord President, who, in turn, is responsible for it to Parliament.

The main headquarters of the Conservancy is in London, but there is a Scottish headquarters in Edinburgh and a Scottish Committee which deals with conservation in Scotland. The Conservancy, consisting of 18 members, mainly biologists, geologists, or geographers, but including 3 Members of Parliament, meets four times a year, one of these meetings being in Scotland. The detailed work is handled by a number of Committees.

As I have already said, the Conservancy lays the greatest stress on the scientific value of nature conservation, in contrast to the "amenity bodies", though it is difficult, or impossible, to

keep the two interests strictly separate. When I am reporting on the merits of a proposed nature reserve, after describing the scientific importance of its flora and fauna, I often find it hard to resist bringing in the scenic beauty of the landscape or the attractiveness of the vegetation, though my allusions to these tend to take on an almost apologetic tone. It is as if I were trying to say "And of course the place really is beautiful as well, though perhaps I ought not to mention the fact".

As no doubt you all know, the central immediate object of the Conservancy is to establish a number of National Nature Reserves chosen as sites of geological or physiographical importance, or as representing leading types of vegetation or assemblages of interesting plants or animals. The sites are either bought outright by the Conservancy (which is not allowed to give more than a sum fixed by the District Valuer as the proper price of the land), or a "Management Agreement" is made with the owner or occupier intended to ensure that the site is managed in accordance with the Conservancy's objects. Probably it is unnecessary with my present audience to explain *why* active management is necessary in the great majority of reserves.

The original list of proposed reserves was between 70 and 80 in England and Wales excluding those of purely geological interest and an original list of 24 in Scotland, but these have been considerably altered. Some originally proposed reserves have proved impossible to secure or no longer worth securing. Other highly desirable areas have come to the notice of the Conservancy since the original list was made. So far as can be foreseen at present the total number of National Nature Reserves in England and Wales is unlikely to reach 100. Of those now on our list, including Scotland, 6 are ready for "declaration", on making which the Conservancy takes over responsibility for the area. With one which has been already declared, these make the Conservancy's total holdings to date 21,615 acres, an acreage mainly accounted for by two large reserves of about 10,000 acres each. Some 3 or 4 more are in an advanced stage of negotiation, and 10 others are under negotiation. Only one, the Beinn Eighe reserve in Wester Ross, has been actually declared. This is a fine tract of 10,450 acres of mountain and moorland with some remains of old self-regenerating native pine forest. The Conservancy have abstained from making "declarations" until arrangements have been completed to take over effective responsibility in each case. But additional declarations are expected soon.[1]

This may seem to some of you rather a poor result of 3 years' work, but actual experience shows how difficult and time-consuming are the negotiations for acquisition or management.

[1]The figures given in this paragraph relate to the end of 1951. At present (March 1953) 9 Reserves have been declared (7 in England and 2 in Scotland), two have been acquired but not yet declared, and 20 more are being negotiated.

Several National Nature Reserves on the Conservancy's list belong to the National Trust, and these are already managed by local committees under the Trust. Good examples are Wicken Fen and Blakeney Point. The Wicken Fen committee, which consists largely of Cambridge biologists, does its scientific job very well, and it seems unlikely that the Conservancy will ever want to interfere with their work. In regard to certain other National Trust reserves management agreements with the Trust will be arranged, by lease or otherwise, ultimate ownership naturally remaining in the hands of the Trust.

Since the different reserves are so various in size and nature the problem of management will be different in each, but a scientific officer of the Conservancy, in some cases resident on or near the reserve, will have to be responsible for each. It is intended to make a thorough survey and study of the animal and plant populations included in the reserves, but in most cases of course this will be the work of many years. Several preliminary surveys have already been made. In some reserves experimental work will be carried on, but care will be taken not to interfere with the general character of the reserve. The 10,000 acre tract of peat moorland in Westmorland, known as the Moorhouse reserve, has been acquired mainly for the purpose of large-scale experiments, which have already been initiated.

In contrast with the Beinn Eighe and Moorhouse reserves, many of the National Nature Reserves are of quite small areas, so that in tota lthey can make but a tiny contribution towards preserving the natural vegetation of the country. This was foreseen by the two committees of the Ministry of Town and Country Planning which sat from 1945 till 1947 and made recommendations for the establishment of National Parks and for the Conservation of Wild Life. Accordingly their reports recommended the designation of large "Conservation Areas", characteristically beautiful tracts of country bearing important vegetation in which care should be taken not to alter the character of the landscape except under the most pressing national necessity, but at the same time not subjecting them to the stricter regime of the National Parks and particularly of the National Nature Reserves. Largely through misapprehension of the aims in view, the institution of Conservation Areas was rather widely opposed, and the Government refused to accept it. This failure involved a serious loss to the chances of preserving the character, depending largely on the vegetation, of some of the most beautiful parts of Britain outside the areas of the National Parks. The Government did however allow the insertion in the National Parks and Access to the Countryside Bill (1949) of clauses that go some little way towards securing the ends in view, both the aims of the Nature Conservancy and those of the National Parks Commission.

Thus Section 23 of the Act reads "Where the Nature Conservancy are of opinion that any area of land, not being land for the time being managed as a nature reserve, is of special interest

by reason of its flora, fauna, or geographical or physiographical features, it shall be the duty of the Conservancy to notify that fact to the local planning authority in whose area the land is situated". And in Section 87 of the Act we find "The Commission [i.e. the National Parks Commission] may, by order made as respects any area in England or Wales, not being in a National Park, which appears to them to be of such outstanding natural beauty that it is desirable that the provisions of this Act relating to such areas should apply thereto, designate the area for the purposes of this Act as an area of outstanding natural beauty . . ." Following paragraphs of the Act provide for full reference of such proposed orders of designation to the local authorities concerned and for adequate publication in newspapers of the proposals to make them. The Commission are enjoined to consider representations made to them as to the effect of a proposed order, while the Minister to whom the proposed order must be submitted may of course refuse to confirm it or may only confirm it with modifications.

Thus, while the Act lays on the Conservancy the duty of notifying local planning authorities of areas considered to be of special scientific interest, but gives them no further powers in regard to such areas, the National Parks Commission may make orders in respect of areas of outstanding natural beauty, but before they can come into force, the orders have to run the gauntlet of local criticism and to face the possibility of the Minister refusing to confirm them. It is thus clear that a real power of preventing any kind of nature conservation, outside the National Parks and the National Nature Reserves, lies with local opinion and with the Minister. How far local opinion can be influenced in favour of conservation, when it threatens or is thought to threaten local interests, remains to be seen.

It is of course true that areas of "outstanding natural beauty" and those of "special scientific interest" do not always coincide, but they very often do, just because they are both likely to be areas of unspoiled wild or semi-wild country, which are both beautiful and also harbour interesting native plants and animals. It is clearly desirable for the Commission and the Conservancy to work together in such cases. A great deal of the time of the scientific officers of the Conservancy has been occupied with designating Section 23 areas during the last two years.

We now come to the actual ways in which the work of the Nature Conservancy may help botanical and ecological interests. So far as plants are concerned there are two particular objects that may be pursued in making nature reserves—first, good and sufficient representation of the distinct types of natural or semi-natural vegetation existing in the country, and secondly, the conservation of areas which contain a number of specially interesting or relatively uncommon species. Both are important and the policy of the Conservancy is to pursue both: in certain cases

the two objects may be fulfilled in a single reserve. The opinion of the Conservancy is rather against making a reserve to preserve a single species, however rare, and a practical objection of course is that the making of such a reserve calls general attention to the existence of the rare species in that place, with the risk of its being over-collected or even exterminated by greedy collectors. It would be interesting and useful to hear the views of experienced field botanists on these matters, and especially as to what if anything can be done to safeguard the localities of very rare species.

Besides scientific work in the reserves, which will be carried out not only by Conservancy scientific officers but also, it is expected, by other qualified scientists such as research workers from the universities, the Conservancy has other duties. In the words of its Charter, its functions shall not only be "to establish, maintain and manage nature reserves in Great Britain, including the maintenance of physical features of scientific interest, and to organise and develop the research and scientific services related thereto", but also "to provide scientific advice on the conservation and control of the natural flora and fauna of Great Britain". This function has been carried out as opportunity offered, in response to requests from Government Departments and others, and also on the initiative of the Conservancy. It is expected to increase considerably in volume as the Conservancy becomes better known and gradually acquires greater knowledge and experience. Among various topics that have thus occupied its attention, the effects on plants and animals of the spraying with weed-killer of grass verges on roadsides, which has been undertaken by certain local authorities, is now being studied by qualified Conservancy agents.

Another important activity is the provision of grants for suitably qualified people—both training grants for students who are working under approved directors and maintenance grants for research workers engaged on approved investigations, mainly of ecological or some ancillary nature. All this entails a great many interviews with candidates for grants, many enquiries and much correspondence.

The Conservancy contemplates the establishment of two research institutes, one in the north and the other in the south of England. Neither of these is yet at work, but suitable premises have been or are being acquired.[2] It is probable, however, that progress with at least one of them will have to be deferred owing to the current urgent need for economy. The originally expected Treasury grant for next year has been cut, though not to such an extent as to cripple the general work of the Conservancy. Simple laboratory accommodation has been provided at

[2]The northern research institute, "Merlewood", near Grange-over-Sands, will begin work in the summer of 1953.

the London and Edinburgh offices of the Conservancy, and there is a library and a collection of maps at each.

To give you some idea of the size and structure of the Conservancy Headquarters organisation, without of course going into details, I may mention that in November 1951 besides the Director-General and the Secretary of the Conservancy there were based on the London headquarters:—

2 Administrative Officers,
a Land Agent,
an Accountant,
6 Office and Technical Assistants,
and
9 Scientific Officers of various grades,

besides Personal Assistants, Clerical staff, typists, etc.[3]

At the Edinburgh headquarters, besides the Director for Scotland, an Administrative Officer and 6 Office and Technical Assistants, there were in 1951 4 Scientific Officers based on Edinburgh.

The Scientific Officers spend, of course, a great part of their time in the field. Up to now they have been mainly engaged in preliminary work such as broad surveys of proposed reserves and areas of "special scientific importance" (Section 23 of the Act), reporting on possibly desirable new reserves, etc. In much of this work they have been generously and substantially helped by biologists who are not officers of the Conservancy. In the future, we look forward to stationing a number of scientific officers in the country, which will be divided into regions with a Regional Officer in general charge of each, while others will be responsible for individual reserves, or groups of reserves. These latter, sometimes called 'wardens' (a term the Director-General disliked—"resident scientific officers" is preferred) will be responsible not only for the management of single reserves or groups of reserves but for study of, and research into, the plant and animal populations, whether done by themselves or by visiting scientists from the universities or elsewhere. Other scientific officers, specialists in various lines of work, will be available for visits to any place where their services are required.

From all this you will have gathered that the Conservancy is still in a very early stage of development. Nothing but preliminary work has yet been done, and that is not by any means finished. One serious lack that has hampered much of the Conservancy's early work has been the great difficulty of getting well qualified senior scientific officers, men (or women), for instance, of the status and experience of lecturers or readers at universities. There are not too many of them in the country with sufficient knowledge of our sphere of work, and those that do exist and have the necessary ecological knowledge and outlook almost invariably, and quite understandably, refuse to abandon

[3]The staff has since been considerably augmented.

an academic career or to give up their specialised researches, however deeply they may sympathise with the work which the Conservancy is trying to do. A particular hindrance has been the lack of a Deputy Director-General, for which post we have been quite unable to find a suitably qualified person who was willing to take it. This lack has deprived the Director-General of essential help and grievously overburdened him with detailed work. As a result of the dearth of senior scientific officers, our recruitment has had perforce to be almost confined to people, many of whom, though often highly talented, have not yet gained the knowledge and practical experience of our flora or fauna required for the training of young and untrained recruits who have just graduated, a necessary function of senior officers. That trouble however should be cured with time.

In an organisation embarked on a completely new kind of task teething troubles can only be expected, and we must look forward to growing pains for some years to come. Besides the hindrances to adequate internal organisation which I have indicated, we are of course faced by the severest competition for the use of land, from the armed services for training grounds, air fields and bombing ranges, from the Forestry Commission for new planting, from the greatly increased quarrying of limestone and gravel digging, and now from the further intensification of pressure for fresh ploughing to produce more food. We are often reproached for wanting to "sterilise" land, since the fruitfulness of biological and ecological knowledge is beyond the ken of too many "practical men". Of course we have to give way to overriding national needs such as the demands of defence and food production, but we should certainly appreciate a better and wider understanding of what we are trying to do and why we are trying to do it.

In the discussion which followed this paper:—

Canon Raven said that it was clear that the Society should continue to place conservation very much in the forefront of its activities. The apathy shown by the public when biological interests are threatened is still far too great. He thought that two matters mentioned by Sir Arthur Tansley should be of special interest to us. The first was the difficult question of how rare species can best be preserved. The alternative policies seemed to be either to notify the precise localities to a national body who would make arrangements for them to be guarded, or to rely on secrecy so that a rigid taboo should be imposed on anyone mentioning the localities where they grow. This was a matter with which our own Society should be very much concerned. The second matter, of special interest to us, was the project for setting up research institutes. It was understandable that more experienced workers hesitated to give up their present careers to undertake this sort of work and that there was a dearth of available recruits. But it was clear that there was something of a swing over to botanical studies among young

people interested in natural history. We should do all we can to encourage them to take up work of the kind undertaken by the Nature Conservancy and to make known the opportunities of applying for posts in their service.

Mr. Lousley said that the Society was already doing a great deal of work towards the conservation of the British flora—which was one of our objects set out in the Rules. Some 40 " threats " were reported by members during 1951 and in all cases we had taken such action as was open to us. Unfortunately much of this work must remain unpublicised for reasons which are obvious, but it cannot be too widely known that we are keenly and actively interested and that we have for some years had a special Committee appointed to deal with conservation. In the case of the more important threats we work in close collaboration with the Nature Conservancy. Members of our Conservation Committee meet representatives of the Nature Conservancy at intervals of six months at a joint meeting when matters of common interest are discussed. He hoped that Sir Arthur Tansley's remarks would lead to even closer collaboration between the Society and the Conservancy than before.

Sir Arthur Tansley replied to the effect that the Society's help in dealing with the problem of the conservation of rare species would be particularly valuable. The Conservancy was faced with great difficulties in knowing how best to deal with localities where rare plants were known to occur (such as Cwm Idwal) or with very scarce species (such as *Cypripedium Calceolus* L. and *Cephalanthera rubra* (L.) Rich.) limited to localities which were kept secret. It was very difficult to know what policy should be adopted.

CONCLUDING REMARKS BY THE PRESIDENT

Canon Raven, in his concluding remarks, said that this had been a very memorable Conference. It was memorable for the extraordinarily high level of interest and ability displayed in the papers which had been read and also in the way in which the whole subject had hung together and moved forward in a definite rhythm. The value and quality of the Conference laid a measure of responsibility on all those who attended.

A great many suggestions had been made by various speakers and he thought it would be extremely valuable if out of these the Society could initiate a country-wide detailed study if this could be done collectively. We should try to develop a limited number of projects rather than to dissipate our resources. As a first step a list should be made of the work which needs to be done. From this list two or three suggestions might be selected for collective work and the support of members invited. It was a reproach that insufficient use had been made in the past of the very wide knowledge available from the Society as a body.

The Conference had opened up a great vision of what the Society might do, and it had drawn attention to certain aspects of field botany which were not apparent before. We must see that these opportunities were not neglected.

FIELD MEETING TO THE NEIGHBOURHOOD OF ASHFORD, KENT

On Sunday, April 6th, a whole day field meeting was arranged with a view to demonstrating some of the species mentioned in papers read to the Conference. Under the leadership of Mr. J. E. Lousley and Mr. D. McClintock, 90 members and friends travelled in two coaches and private cars to Hothfield, near Ashford, Kent.

Shortly before reaching Swanley the coaches passed sandy fields where "shoddy" is used as a manure (cf. p. 160) and 22 species of wool aliens have been collected (*London Naturalist*, **28**, 27, 1949). The party stopped at the southern end of Mereworth Woods to examine a large colony of *Acaena anserinifolia* (Forst.) Dr. which grows here abundantly in competition with native plants (see p. 152). Fruiting heads were collected and the long barbed spines examined.

At Ripper's Cross near Hothfield, *Thlaspi alliaceum* L. was seen in abundance in the locality where it was first found in May 1923 (see p. 148, and *J. Min. Agric.*, **30**, 535-8, 1923; *Rep. Bot. Soc. & E.C.*, **7**, 28-29, 1924; *J. Bot.*, **62**, 306-7, 1924). In spite of the heavy snow which fell about a week before the meeting, the plants were in full flower, and a few had formed seed-pods (Plate VI). Although the party scattered and examined many fields, no appreciable extension of the known range was reported. The plant was found in two fields on the west side of Bear's Lane in arable and hedgerows, and in much smaller quantity in two fields on the east side of the lane and in Bear's Lane Wood. The greatest distance between the plants observed was 450 yards.

Later in the afternoon the coaches proceeded to Boxley Warern, near Maidstone. Here *Buxus sempervirens* L. was formerly abundant, for John Ray, in 1695, wrote ". . . I find in the notes of my learned friend Mr. John Aubrey that at Boxley (in Kent) there be woods of them" (Ray in Camden, *Britannia*, 262). In recent times the Box here has not been abundant and much of the remaining colony was destroyed during the war. It grows on very steep chalky slopes in a habitat similar to the one at Box Hill (cf. p. 187), and the village is apparently named after it. Unfortunately only a few of the party were successful in finding the remaining trees in the short time available.

Beneath some of the ancient trees of *Taxus baccata* L., plants of *Euphorbia Lathyris* L. were seen in a locality far from houses, which has been known since 1862. Dr. Warburg's remarks of the previous day were recalled when several old trees of *Quercus Ilex* L. were found amongst characteristic native trees and shrubs of the chalk, and in places where they were very unlikely to have been planted. Prof. Tutin found a seedling and thus confirmed that the *Quercus* was regenerating.

Thlaspi alliaceum L. at Ripper's Cross, Hothfield, Kent.

Photos by C. N. Pope

On the return journey the coaches passed Forstal Quay, and crossed the Medway at Aylesford where *Scirpus triqueter* L. was formerly plentiful. The colony seen by J. E. Lousley in 1934 was destroyed by dredging shortly afterwards and the species now appears to be extinct here. Mention of an extinction as the last example of the Conference was a fitting reminder of the importance and urgency of conservation. The loss of some species is inevitable owing to "improvements" of economic importance which botanists cannot hope to resist. To save others, where it is possible to take effective action, is a matter of the greatest importance. Additions to "The Changing Flora of Britain" can take their course: it is the duty of everyone interested to help in the work of keeping our losses as low as possible.

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